FOREST Science

A QUARTERLY JOURNAL OF RESEARCH AND TECHNICAL PROGRESS

Volume 7-Number 1-March, 1961

PUBLISHED BY SOCIETY OF AMERICAN FORES

WASHINGTON,

FOREST SCIENCE is published quarterly by the Society of American Foresters with the cooperation of forestry research and educational organizations.

The journal assumes no responsibility for the statements and opinions expressed by contributors. The editors cannot be responsible for loss or damage of manuscripts and accompanying matter.

Correspondence concerning manuscripts submitted for publication and other editorial matters should be addressed to Dr. John W. Duffield, Industrial Forestry Association, Nisqually, Washington.

Other correspondence, including subscriptions, remittances, reprint orders, and inquiries concerning the status of manuscripts accepted for publication, should be addressed to the Society of American Foresters, Mills Building, Washington 6, D. C.

Subscription price is $6.00 per year for complete volumes (one per calendar year), and $2.00 for single number. Add $0.25 for postage to Canadian addresses and $0.50 for postage to other foreign addresses.

The pages of FOREST SCIENCE are open to all qualified contributors. Preference will be given to papers devoted to the presentation and discussion of the results of original research. Authors are expected to bear the cost of that portion of their papers in excess of 16 printed pages in length and of tabular and illustrative material constituting more than 20 percent of the length of the paper.

Papers of 32 printed pages or longer (approximately 20,000 words or about 65 pages of manuscript) will be considered for publication as *Forest Science Monographs* under the same editorial procedures followed for shorter contributions. The monographs will be printed with covers, distributed without charge to the subscribers as supplements to regular issues, listed in the table of contents of the appropriate issue of FOREST SCIENCE, and included in the annual index. The entire cost of printing and mailing each monograph (but not editorial costs) must be met by the author or other agency.

Board of Edi

John W. Duff

Industrial Forestry Associ
Nisqually, Washi

Henry Cle
F. H.
Society of American For

V. L. Ha
Forest Service, U. S. Department of Agricu

Business Mana
Miss L. Audrey Wa
Society of American For

Copyright, 1960, by the Society of American Fores

Second class postage paid at Washington, D. C., and at additional mailing of

Printed in the United States of Am

FOREST *Science*

A Quarterly Journal of Research and Technical Progress

Flooding and Drainage Effects on Slash Pine and Loblolly Pine Seedlings
Laurence C. Walker, R. Lamar Green, Joe M. Daniels 2

Seasonal Variation in the Moisture Content of the Green Leaves of Mountain Laurel
William E. Reifsynder 16

Vegetative Indicators of Rate of Height Growth in Ponderosa Pine
R. Daubenmire 24

Crown Competition—A Measure of Density
John E. Krajicek, Kenneth A. Brinkman, Samuel F. Gingrich 35

The Influence of Gibberellic Acid on Growth and Fiber Length of Quaking Aspen
Dean W. Einspahr, J. P. van Buijtenen 43

Properties of Some Random and Systematic Point Sampling Estimators
Marshall N. Palley, Leah G. Horwitz 52

Organic Layers in Minnesota Aspen Stands and Their Role in Soil Improvement
Joseph H. Stoeckeler 66

Equations for the Description of Past Growth in Even-Aged Stands of Ponderosa Pine
Charles F. Cooper 72

Effects of Photoperiod and Source on Seedling Growth of Eastern Hemlock
Hans Nienstaedt, J. S. Olson 81

REVIEW: Forest Fertilization 23.

ERRATUM: 96.

Advisory Board

Henry Hellmers
George R. Staebler
Ellis T. Williams
John A. Zivnuska
Noel D. Wygant
François Mergen
Harry G. Smith
Donald P. White
George H. Hepting
T. T. Kozlowski
Leslie W. Orr
Robert Zahner

Volume 7
March, 1961
Number 1

Flooding and Drainage Effects on Slash Pine and Loblolly Pine Seedlings

BY
LAURENCE C. WALKER
R. LAMAR GREEN
JOE M. DANIELS

SLASH PINE (*Pinus elliottii* var. *elliottii* Engelm.) and loblolly pine (*P. taeda* L.) seedlings appear to have a high degree of tolerance to poor drainage and flooding. This tolerance is important in the silviculture of the southeastern Coastal Plain flatwoods where imperfectly drained Bladen clay loam and related soils predominate. Approximately 75 percent of the area in these soils, in which both surface and internal drainage are poor, is devoted to woodlands. Pines are the most valuable species, yielding high quality timber, pulpwood, and naval stores. Generally, the pines are restricted to the better drained sites while less valuable hardwoods are the dominant species in low-lying, poorly drained zones. Throughout this region, extensive areas occur in which, when drained, stands of pine develop from natural seedfall. Both stocking and growth of pines may be substantially increased by providing adequate drainage.

Trousdell and Hoover (1955) are mindful that "in years with heavy spring rainfall, it may be difficult to regenerate pine stands on some poorly drained sites by clearcutting systems because of standing water on the prospective seedbed during the germination period." Wet conditions also result in death of residual seed trees.

In addition to silvicultural implications, high water causes costly and unpredictable logging operations. Heavy machinery makes logging roads impassable, and the puddling of soil by compaction reduces productivity of a site.

No major research has been directed at determining effective and economical drainage coefficients for woodlands and, therefore, the full benefit of particular water removal rates to both tree growth and logging remain speculative. Agricultural and civil engineers requested to design woodland drainage systems have little data on which such designs may be based. Nevertheless, there is much active interest in woodland drainage and engineers are receiving an increasing number of requests for assistance in the layout of water-removal systems.

This paper presents the results of an effort to determine the effect of (1) continuous flooding, (2) continuous drainage,

---

L. C. Walker is Associate Professor, School of Forestry, University of Georgia; R. L. Green, now head of the Department of Agricultural Engineering, University of Maryland, was Superintendent of the Southeastern Tidewater Experiment Station at Fleming, Georgia, during the course of this study. J. M. Daniels is an engineering aid at the station. Journal Series No. 119 of the College Experiment Station of the University of Georgia College of Agriculture Experiment Stations. The study, a cooperative project of the University and the Soil and Water Conservation Research Division, Agricultural Research Service, U. S. Dept. Agric., was supported in part by the Georgia Forest Research Council. Manuscript received Jan. 20, 1960.

and (3) three drainage coefficients upon survival and growth of slash and loblolly pine seedlings. A drainage coefficient is the amount of water, in inches, removed from a site during a 24-hour period.

Literature Review

The effect of deep channel drainage on slash and loblolly pines in the North Carolina coastal area, where ditching lowered water tables to a distance as great as 1000 feet, has been reported by Pruitt (1947) and Schlaudt (1955). Height growth was increased from the ditch to a distance of 500 feet, and soil physical properties were improved. The slightly detrimental growth effect of flooding upon shortleaf (*Pinus echinata* Mill.), loblolly and pond pines (P. *serotina* Michx.) is reported by Hunt (1951). Although loblolly and shortleaf pines made more growth than pond pine in sand cultures flooded for various periods, in general, all seedlings proved unusually resistant to injury. After 12 weeks, slightly reduced growth was recorded for seedlings continuously flooded with standing water. Flooding for three months did not permanently damage root systems; but after ten months, the roots appeared so badly injured that the plants would probably have died if the soil dried below field capacity. Gaiser[1] also reported loblolly pine to be more resistant than pond pine to flooding injury. Both species made better growth in soil intermittently flooded for short periods, 2 days out of 9, than in soil maintained at field capacity.

Prompt removal of excess water from small stagnant bogs beneficially influenced leader growth of black spruce *Picea mariana* (Mill.) B.S.P. and balsam fir (*Abies balsamea* L. Mill.) saplings. Acceleration of growth decreased with distance from the drainage ditch in this Michigan study (Satterlund and Graham 1957).

The effect of flooding on seedling survival is exhibited even for such hydrophytes as baldcypress, *Taxodium distichum* (L.) Rich. Ten to 12 days submergence may cause death. Demaree (1932) observed that this species must grow to sufficient height during the first year to stay above floods during the second year except for a very few days at a time.

Other species detrimentally affected by high water include red pine (*Pinus resinosa* Ait.) (Stone *et al.* 1954), conifers of the Lake States' region (Ahlgren and Hansen 1957), and numerous hardwoods in the upper Mississippi River (Green 1947, Yeager 1949) and adjacent to northern Swiss lakes (Kuster 1948). Ahlgren and Hansen's work showed no uniformity in the effect of duration of submergence on subsequent terminal growth. Trees flooded for less than 28 days in many cases showed as much growth reduction as trees flooded for longer periods.

Redox potential measurements show that conditions favoring oxidation and/or reduction in a soil in the absence of oxygen are not readily removed by additions of oxygen deficiency were considered to be waterlogging on plant growth may persist for some time after the soil is drained, and even temporary flooding may be injurious to plant growth (Scott and Evans 1955).

The variation among species in ability to withstand flooding is, of course, ancient knowledge, but the mechanics of continued growth are speculative. Kramer (1949) and Leyton and Rousseau (1958) note that *Salix* roots, for instance, grow and absorb water in almost complete absence of oxygen. *Heliotropium*, on the other hand, ceased water absorption 15 hours after the soil atmosphere was replaced by nitrogen. Carbon dioxide toxicity and oxygen deficiency, were considered to be the causes. Reduced water absorption might be due to lessened metabolic activity of roots or physical changes in permeability. It is accompanied by retarded transpiration, photosynthesis, and mineral absorption, and finally manifested as wilting. Kozlowski (1958) and Bergman (1920) reported that in flooded soils, absorption of water by roots often decreased and lagged

[1]Gaiser, R. N. Unpublished thesis. Duke University, 1947.

behind transpiration, causing leaves to dry out.

Further evidence that absorption is not the only factor inducing injury was presented by Kramer (1933) to the effect that loblolly pine seedlings absorbed water and appeared uninjured for two weeks after roots were killed. As Kramer later stated (1951), lack of water cannot explain the curvature of leaf tips, hypertrophy, nor development of adventitious roots. These changes take place more likely in turgid, growing tissues. He suggested that flooding injury may be related to disturbance of translocation of carbohydrates and possibly of hormones. Interference with downward translocation due to lack of oxygen "results in an accumulation of carbohydrates in the lower part of the stem, near the water line, causing hypertrophy and the development of adventitious roots." Kramer considers it unlikely that nutrient deficiencies are an important factor in flooding injury but, rather, he suggests that poisoning by toxic substances moving up from dying roots may be the reason. Loblolly pine transpiration, according to Parker (1950), increased to 125 percent of the expected rate for a week after flooding, then decreased constantly to 60 percent when drained 4 weeks after flooding, then a week later to 20 percent.

Water-logged soils high in organic matter, typical of many southeastern coastal forest sites, may also contain toxic quantities of iron, sulphides, and manganese, built up as a result of the presence of CO_2 released in biological activity (Kramer, 1949). Chlorosis and wilt of leaves of flooded plants is known to decrease with removal of CO_2 from soil solutions (Jackson, 1956).

Dean (1933) found aeration important in the production of root hairs and lateral roots, even for aquatic plants. In studying hydrophytes, Bergman (1920) reported that as soon as the plants growing beneath the surface of swamp water showed signs of wilting, supplying air or oxygen would result in restoration to normal.[2]

Description of the Site

The study was conducted at the Southeastern Tidewater Experiment Station, south of Savannah, Georgia. The natural forests of the area, known as the flatwoods, are principally loblolly pine, intermingled with willow oak, longleaf pine, sweetgum, and reeds.

The Bladen clay loam of the area is a low humic gley soil formed from thick beds of acid clay. It is noted for its slow internal drainage and plastic *B* horizon. The principal type of the series is fine sandy loam with slightly lighter color of the *A* horizon than the yellow-brown mottling typical of the underlying *B*. The *A* horizon is 4 to 10 inches thick and strongly acid. The texture of the *B* horizon varies from sandy clay to clay. When dry, it is extremely hard, shrinks and cracks, and breaks into angular blocks. The *B* horizon is about 6 feet deep in the study area. Bladen soils join areas of tidal marsh and occur on broad level flats with a few areas in ponded positions from 4 to 30 feet above sea level. Drainage canals are considered essential for agriculture. The impermeability of Bladen soil is indicated by the very slight lowering of the water table at stand edges in contrast to the sharp decline one-half chain within a stand (Trousdell and Hoover 1955).

Studies with replicated lines of drawdown wells, about 500 yards from the area of the experiment reported here, showed that a drainage ditch five feet deep had no effect on ground water profiles at distances greater than 12 feet from the ditch. Other studies indicate wide variation in soils referred to as the "Bladen Series" along the South Atlantic Coast.

---

[2]A new book "Physiology of Trees" by P. J. Kramer and T. T. Kozlowski (McGraw-Hill, 1960), published after submittal of this paper, gives an excellent literature review of this subject.

On Bladen and similar soils, differences in vegetative stocking are reported as affecting the drawdown rates of water tables during a rain-free summer period. The rates ranged from 0.14 to 0.09 feet per day, depending upon the proximity of the water table to root concentrations. Drawdown during the growing season, caused principally by evapotranspiration, appeared to be three to four times that of drainage alone.[3]

Rainfall at the study area for 1957 was 52 inches; and for 1958, 48 inches.

Description of Main Experiment

One-year-old slash and loblolly pine seedlings were planted at 2 x 2 foot spacing in mid-February 1957, in previously prepared 12 x 24 foot diked and ditched plots. The soil was undisturbed at time of planting. The whole plots were divided into 2 split plots, each randomly assigned 25 trees of one species. Nursery-grown stock from seed originating in the coastal area was used.

A severe four-month drouth preceded planting. Therefore, to improve survival chances, all seedlings were watered within five days. Twenty-four slash pines and 13 loblolly pines, less than 3 percent of the 1350 trees planted, died and were replaced by early March. Between planting and beginning of water treatments on May 31, average height of slash pine seedlings had increased 3.5 inches (to 7.5 inches) while loblolly had grown an average of 5.9 inches (to 11.8 inches). All growth measurements were made to the nearest inch—from the ground to the terminal bud. The difference in initial size of the two species was of such magnitude that subsequent results were expected to be strongly biased in favor of loblolly pine (Table 1).

Initial watering following planting, replanting, and favorable growing conditions for three and one-half months prior to establishment of water treatments insured strong, vigorous plants for study.

FIGURE 1. *A drainage plot at the time treatments began.*

The design consisted of 3 blocks of nine randomized treatment plots each.

Treatments (Fig. 1) were:

(a) Water level maintained 8 inches above mean plot elevation (+8),
(b) Water level maintained 4 inches above mean plot elevation (+4),
(c) Water level maintained at mean plot elevation (±0),
(d) Water level maintained 4 inches below mean plot elevation (−4),
(e) Water level maintained 8 inches below mean plot elevation (−8),
(f) Water applied to a three-inch depth at three-week cycles. Outlets were lowered daily ⅛ inch (drainage coefficient), plus evaporation (dr ⅛),
(g) Same as (f) with ¼-inch drainage coefficient (dr ¼),

[3]Gallup, L. E. Unpublished thesis. North Carolina State College, 1954.

(h) Same as (f) with ½-inch drainage coefficient (dr ½),
(i) Uncontrolled check plot on undisturbed soil (ck).

Flooding treatments were begun in early June 1957 and maintained throughout the balance of the two-year experiment, except for (a), which was concluded at the end of the first year. Drainage treatments (f), (g), and (h) were suspended in November 1957 and resumed on March 26, 1958, at the first indication of the breaking of dormancy.

Water from an artesian well was supplied through plastic piping of one-inch mains and three-quarter-inch laterals. Water levels were controlled by inverted siphon outlets from dikes or ditches which encircled the plots. The water supply to each plot had independent manually-operated inlet valves. The constant water level treatments were maintained to offset evaporation, transpiration, and seepage. Valves were adjusted to provide slight water movement through overflow outlets which had sufficient capacity to remove excess rainfall within 24 hours. Prior to lowering outlets in the drainage coefficient plots, evaporation was measured in a standard Weather Bureau pan for the preceding 24 hours and the amount added to the drainage coefficient.

Check plots adjacent to the diked areas received no treatment other than watering at time of planting to insure survival. However, ponding occurred on these plots for periods of a week or more on several occasions after heavy rains, but the plots were never flooded to three-inch depths, as were the drainage coefficient plots at three week intervals. The check plots were then at an intermediate soil moisture level throughout most of the growing season. The maximum variation in elevations within plots was 0.48 foot. Most plots did not vary more than 0.2 foot in elevation.

Movement of water through Bladen soil is known to be very slow. Thus, it was not generally necessary to puddle core trenches under levees, which were 18 inches high with an 18-inch top width and a 1:1 side slope. Where fill material did not bond with top soil, causing seepage along lines of cleavage, cores were puddled through the top soil. Crayfish (*Cambarus* sp.) were a problem on some plots: they tunneled under levees, making holes over an inch in diameter through which water temporarily escaped.

Survival counts were taken monthly and heights of seedlings measured at time of planting and periodically thereafter.

Water temperatures on +4 and +8 plots were recorded on five days each month and whenever atmospheric temperatures exceeded 90°F the first year, and about every three days during the second growing season. At the same time —about 3:30 pm—air temperatures were observed above the plots.

Determination of dissolved oxygen in standing (semi-stagnant) water was made for samples withdrawn on three occasions from the +8 treatments. For comparison, dissolved oxygen was determined for artesian water (source for treatments), water from a nearby running stream, stagnant water ponded in the forest, and stagnant water in an open field. The Solvay (1957) Method 22 (Winkler $MnSO_4$) method was employed.

The study was terminated after two years because it was evident that, on the plots with better growth, crowns of seedlings would be interlocked before the end of the third growing season.

Supplementary Study

Because few seedlings survived in the three plots flooded to eight-inch depths from June 1957 to January 1958, further observations would serve no useful purpose. These plots were then drained on January 30, 1958, and a supplementary study installed in mid-February to determine (a) whether slash and loblolly pine seedlings can survive if planted on waterlogged Bladen soil immediately after surface drainage is provided, and (b) whether

TABLE 1. Mean number of surviving seedlings with drainage and constant water level treatments. (25 = 100 percent). (Number of days refers to the time since treatment began on May 31, 1957.)

No. days	Species	Constant water levels +8	+4	±0	−4	−8	Drainage coefficients ⅛	¼	½	check	LSD[1] 5%	1%	Anal. of Vairance[1] Treat.	Sp.	Sp. x Tr.
41	Slash	23.0	24.3	24.3	23.0	22.7	23.7	23.3	23.3	23.0					
	Loblolly	24.7	25.0	24.7	25.0	25.0	24.3	24.7	24.7	25.0	2.2	3.0			
	S + L	23.8	24.7	24.5	24.0	23.8	24.0	24.0	24.0	24.0	1.9	3.9	ns	**	ns
68	Slash	17.0	24.3	24.0	23.0	22.7	23.7	22.7	23.0	22.7					
	Loblolly	24.7	25.0	24.7	25.0	25.0	24.3	24.7	24.7	25.0	3.1	4.3			
	S + L	20.8	24.6	24.3	24.0	23.8	24.0	23.6	23.8	23.8	0.9	1.2	**	ns	*
101	Slash	5.3	23.7	23.0	22.7	22.3	23.3	22.7	22.3	22.7					
	Loblolly	22.7	24.3	24.7	25.0	25.0	24.3	24.7	24.3	24.7	3.6	4.9			
	S + L	14.0	24.0	23.8	23.8	23.6	23.8	23.6	23.3	23.6	2.4	3.3	**	**	**
133	Slash	7.7	23.0	22.7	22.7	21.3	22.7	22.7	22.3	22.3					
	Loblolly	19.3	22.7	24.3	25.0	25.0	24.3	24.7	23.3	24.3	5.0	6.8			
	S + L	13.5	22.8	23.5	23.8	23.2	23.5	23.6	22.8	23.3	3.1	4.2	**	**	ns
166	Slash	7.7	20.7	21.7	22.7	21.3	22.7	22.3	22.3	22.3					
	Loblolly	16.0	17.7	24.3	25.0	25.0	24.3	24.7	23.0	24.3	5.5	7.6			
	S + L	11.8	19.2	23.0	23.8	23.2	23.5	23.5	22.7	23.3	4.6	6.3	**	*	ns
206	Slash	3.0	17.7	20.3	22.7	21.3	20.3	21.3	19.7	22.0					
	Loblolly	13.7	15.3	23.3	25.0	25.0	24.3	24.3	22.3	24.3	3.4	4.7			
	S + L	8.3	16.5	21.8	23.8	23.2	22.3	22.8	21.0	23.2	5.8	8.0	**	**	**
245	Slash		14.0	19.3	22.0	21.3	20.0	18.7	18.0	21.7					
	Loblolly		14.7	23.3	25.0	25.0	24.3	24.0	21.7	24.3	3.5	4.9			
	S + L		14.3	21.3	23.5	23.2	22.2	21.3	19.8	23.0	3.1	4.4	*	**	ns
277	Slash		18.0	19.7	22.0	21.0	21.7	20.7	21.3	21.3					
	Loblolly		10.0	23.0	25.0	24.7	24.3	24.0	21.3	24.3	4.7	6.4			
	S + L		14.0	21.3	23.5	22.8	23.0	22.3	21.3	22.8	4.3	6.0	**	ns	*
304	Slash		18.7	19.3	21.7	21.0	22.0	22.0	20.3	21.0					
	Loblolly		9.7	22.3	24.7	24.7	24.3	24.0	20.3	24.3	4.6	6.3			
	S + L		14.2	20.8	23.2	22.8	23.2	23.0	20.3	22.7	4.4	6.0	**	ns	*
335	Slash		18.7	19.3	21.7	21.0	21.7	22.3	20.7	21.3					
	Loblolly		9.0	22.0	24.7	24.7	24.3	24.0	20.7	24.3	4.5	6.3			
	S + L		13.8	20.7	23.2	22.8	23.0	23.2	20.7	22.8	2.9	4.1	**	ns	**
369	Slash		18.7	18.7	21.7	21.0	21.7	22.0	20.0	21.0					
	Loblolly		9.0	22.0	24.7	24.3	24.3	22.3	20.7	24.3	4.1	5.6			
	S + L		13.8	20.3	23.2	22.7	23.0	22.2	20.3	22.7	4.3	6.0	**	ns	**
398	Slash		18.3	18.7	21.7	21.0	21.7	21.3	19.7	21.0					
	Loblolly		8.7	21.7	24.7	24.3	24.3	22.3	20.7	24.3	4.2	5.8			
	S + L		13.5	20.2	23.2	22.7	23.0	21.8	20.2	22.7	3.1	4.3	**	ns	**
431	Slash		17.7	18.0	21.7	21.0	21.7	21.3	19.7	21.0					
	Loblolly		8.3	21.7	24.7	24.3	23.7	22.0	20.7	24.3	4.4	6.1			
	S + L		13.0	19.8	23.2	22.7	22.7	21.7	20.2	22.7	3.1	4.3	**	ns	**
459	Slash		17.3	17.7	21.7	21.0	21.3	21.3	19.7	20.0					
	Loblolly		8.3	21.7	24.3	24.3	23.7	21.7	20.7	24.3	4.2	5.8			
	S + L		12.8	19.7	23.0	22.7	22.5	21.5	20.2	22.2	3.1	4.4	**	ns	**
489	Slash		16.3	17.7	20.7	20.7	21.0	20.7	19.7	19.7					
	Loblolly		7.7	21.3	24.3	23.7	23.7	20.7	20.7	24.3	4.7	6.5			
	S + L		12.0	19.5	22.5	22.2	22.3	20.7	20.2	22.0	3.1	4.2	**	ns	**
518	Slash		16.0	17.3	20.7	20.7	21.0	20.7	19.3	19.7					
	Loblolly		7.0	21.3	24.3	23.7	23.3	20.3	20.7	24.3	4.5	6.2			
	S + L		11.5	19.3	22.5	22.2	22.2	20.5	20.0	22.0	2.9	4.1	**	ns	**
550	Slash		16.0	17.0	20.7	20.3	21.0	20.3	18.3	19.7					
	Loblolly		6.3	21.3	24.0	23.7	23.3	20.3	20.7	24.3	4.2	5.8			
	S + L		11.2	19.2	22.3	22.0	22.2	20.3	19.5	22.0	3.5	4.9	**	ns	**

[1]LSD = Least Significant Difference at the respective levels for recording statistical variance between any two figures in the line, or lines, for which the LSD's are given. One asterisk indicates 5 percent level and two asterisks indicate 1 percent level. Replication was not significant at all periods.

seedlings, subjected to 8-inch flooding for periods of 2, 4, and 8 weeks will survive after drainage. As only these three plots were available, range in duration of flooding was sought, rather than replication. One hundred seedlings of each species were planted in each plot at 1 x 1 foot spacing. During the two-week interim between draining and planting, a crust formed on the soil which would temporarily support a man; but the trampling during hand-planting left the soil mushy. Machine planting would have been impossible under these conditions. As in 1957, seedlings were permitted to grow until June before being subjected to flooding. Loblolly pine seedlings were from seed from a single tree, slash pine seedlings were common stock.

Results and Discussion

Survival. Few seedlings died during the first 41 days, from May 31 to July 11, even on plots flooded to a depth of 8 inches above mean plot elevations. Nevertheless, highly significant differences were noted between species (Table 1). Appreciable mortality was first observed for slash pine on the +8 plots 68 days after treatment began. For loblolly pine, it was observed at 133 days on both +4 and +8 plots. Of the slash pine seedlings, 64 percent survived at the end of the experiment.

Seedling heights seemed important to survival. For the first year, loblolly pine seedlings survived better than slash pine under flooded conditions, possibly because the loblolly pines were taller when treatments began. By rearranging height and survival data, we found a relationship between height of terminal bud above the water surface and the time required for flooding to kill pine seedlings during the first year (206 days), regardless of species (Fig. 2). Much of the difference in survival occurred in the +8 treatments, where slash pine heights averaged 0.9 inch less than the water level. The loblolly seedlings for this treatment averaged 4.0 inches above the water. Slash pine so treated (+8) had survival rates significantly lower (1 percent level) than for all other treatments. Loblolly pine seedlings averaging 6.6 inches above water level also had lower survival rates than those which averaged 11.0 inches above that point. Between other seedling heights, as related to water level, no significant differences either within or between species were apparent. The interaction between species and treatments, although statistically significant in August (68 days), September (101 days), and December (206 days) of the first year is, therefore, not of real importance. It is possible that the same reasoning would hold for the significant interaction found at the first measurement of the second year (245 days).

Following the first 41 days of treat-

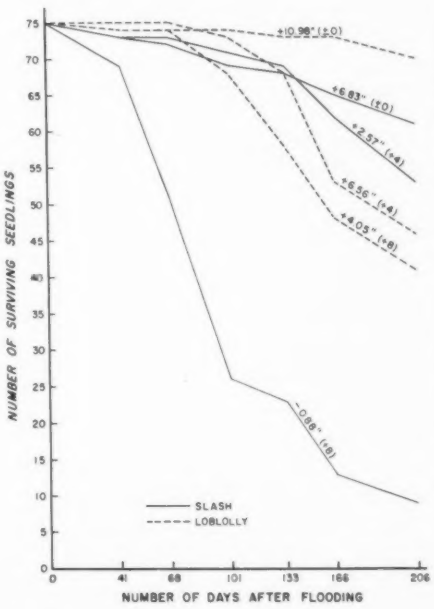


FIGURE 2. *Relation between height of seedlings above water surface and their survival with respect to time. Treatments are shown in parentheses. The number of seedlings at the time flooding began was 75 in each case. L.S.D.—5 percent = 8.6; 1 percent = 11.6.*

ment, trees died at an increasing rate on plots flooded to depths of 4 and 8 inches and by 206 days practically all seedlings on the +8 plots were dead. Only 66 percent survived on the +4 plots. On the ±0 plots, survival was 87 percent, and all other treatments were above this acceptable minimum. In the 27 days following the first 41, from July 11 to August 7, the differences between treatments taken together became highly significant and remained so. At no time during the first growing season was there a significant difference in survival between the check plots, the three drainage coefficient treatments, or the three constant water level drainage treatments (±0, −4, −8).

The amount of drainage appeared unimportant to survival at the end of the experiment, as long as seedlings were not continuously flooded. In December 1958, 550 days after establishing water control treatments, there were still no significant differences between treatments or species except for the +4 treatment. For slash pine, survival was definitely inferior on the +4 to the −4, −8, dr ⅛, and dr ¼ plots. But no significance was shown between these two drainage treatments and the dr ½ treatments. For loblolly pine, the +4 plots exhibited poorer survival than did all other treatments. (It will be recalled that the +8 plots were previously abandoned.) Slash pine survival was better than loblolly pine (1 percent level) on the +4 treatments and inversely so on the ±0 plots. Yet, for all treatments combined, species differences were not apparent.

In the supplementary study average survival 4 months after planting, when treatment began on June 6, was 69.3 percent for slash pines and 96.0 percent for loblolly pines. This is similar to the main study survival observation—that the slash pine stock employed here apparently required a more favorable planting environment than did the loblolly pine for equal chances of survival. Loblolly pine seedlings temporarily withstood inundation

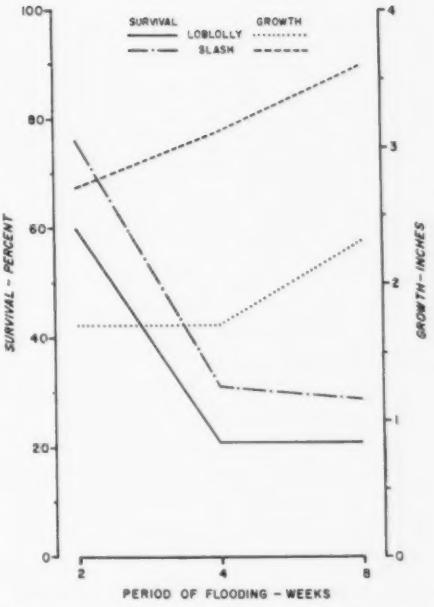


FIGURE 3. *Survival and growth of seedlings 18 weeks after the three 8-inch flooding treatments ceased (supplementary study).*

better than slash pine. On water-logged soil flooded to depths of 8 inches—approximately the height of terminal buds—survival was better for loblolly pine only as long as submergence continued (Table 3). This held especially for the 4- and 8-week inundation periods. The initial advantage of loblolly pine was then offset by its higher mortality after drainage began. In all three plots, survival of slash pine 6 weeks after the plots were drained slightly exceeded that of loblolly pine, and this difference persisted. Eighteen weeks after the 2-week flooding period was over, slash pine seedling survival was 76 percent and loblolly pine 60 percent. This indicates that trees with an 8-inch inundation for 2 weeks in June may have such a low survival as to require subsequent replanting (Fig. 3). It is possible, however, that flooding earlier in the year, when water temperatures are lower, would have less severe effects.

Growth. Height growth of pines in the flatwoods continues throughout the season in which pines are normally considered dormant. While it was first believed that early October approximates the inception of winter dormancy in the southeastern Tidewater area, trees in several plots measured on November 13, 1957 had grown twice as much in the 33 days since October 11 as in the previous 133 days. Because these data contradicted anticipations, it was decided to make growth measurements monthly. As survival was low for plots flooded to a depth of 8 inches, growth data for these treatments are omitted to permit a more accurate analysis of variance between other treatments.

On October 11, 133 days after establishment of water treatments, the first height measurements were made and net growth of surviving trees determined. At that time slash pine height growth ranged from 0.3 inch on the ±0 plots to 3.0 inches on the −8 plots. Loblolly pine averaged 0.7 inch on the ±0 treatment and 4.0 inches on the check plots. Treatment responses were significantly different (1 percent level), as was the interaction between species. Species x treatment interaction, however, was significant at the 5 percent level, while variation among replicates of the same treatment was not.

FIGURE 4. *Slash pine seedlings at conclusion of the experiment. From left to right: ±0, +4, −8, and check treatments.*

The −8 treatment was best for slash and loblolly pine height growth combined. Highly significant differences were found between the +4 and −4, +4 and −8, +4 and ck, ±0 and −4, ±0 and −8, ±0 and ck, −4 and dr ½, −8 and dr ½, and ck and dr ½ treatments. For each succeeding date of measurement, and for each species, these statistical variances are readily determined from the figures on least significant difference (LSD) in Table 2.

Treatment differences remained highly significant throughout the study. The statistical difference between species disappeared after the first measurement; but early in the second year, when replication variance appeared, species difference became highly significant and remained so until the conclusion of the experiment. Near the end of the study replication variance was found highly significant. No consistency was noted for the species x treatment interaction.

At the end of the study, slash pine height growth ranged from 4.4 inches on the ±0 plot to 19.7 inches where drainage was to a depth of 8 inches (Fig. 4). Loblolly pines behaved similarly, being smallest (6.2 inches) on the ±0 plot, and 21.8 inches on the −8 plot. The trend in growth for slash pine from least to best was: ±0, dr ¼, +4, dr ½, dr ⅛, ck, −4, and −8. For loblolly, it was ±0, dr ¼, dr ½, dr ⅛, +4, ck, −4, and −8. Extreme plot conditions at the end of the tests are shown in Figure 5.

Throughout the first year loblolly pine seedling growth was best on the check plots. Not until over 15 months (459 days) had elapsed was the −8 treatment found to be better. Perhaps the second growing season was more typical for judging the effect of poor natural drainage

TABLE 2. Average growth, in inches, of surviving seedlings with drainage and constant water level treatments. (Number of days refers to the time since treatment began on May 31, 1957.)

No. days	Species	Constant water levels				Drainage coefficients			check	LSD[1]		Anal. of Variance[1]			
		+4	±0	−4	−8	⅛	¼	½		5%	1%	Repl.	Treat.	Sp.	Sp. x Tr.
133	Slash	0.6	0.3	2.0	3.0	1.4	0.6	0.6	1.6						
	Loblolly	1.0	0.7	2.6	2.0	1.7	1.6	0.9	4.0	1.4	1.9				
	S + L	0.8	0.5	2.3	2.6	1.6	1.1	0.7	2.8	0.9	1.3				
												ns	**	**	*
166	Slash	2.0	1.7	3.7	4.1	2.7	1.6	2.0	2.4						
	Loblolly	1.7	1.9	4.1	3.1	2.9	2.6	1.9	5.1	1.9	2.6				
	S + L	1.8	1.8	3.9	3.6	2.8	2.1	1.9	3.8	1.3	1.9				
												ns	**	ns	ns
206	Slash	2.9	2.2	4.2	5.0	3.7	2.5	2.7	3.3						
	Loblolly	2.7	2.2	4.4	3.7	3.2	3.0	2.3	5.7	1.5	2.1				
	S + L	2.8	2.2	4.3	4.4	3.4	2.7	2.5	4.5	0.9	1.2				
												ns	**	ns	ns
245	Slash	4.1	2.8	4.5	5.4	4.0	3.4	3.4	3.8						
	Loblolly	3.0	2.7	4.7	4.2	3.4	3.3	2.6	6.1	1.4	1.9				
	S + L	3.6	2.7	4.6	4.8	3.7	3.3	3.0	4.9	1.0	1.3				
												ns	**	ns	*
277	Slash	3.2	2.7	4.5	5.5	3.7	3.0	2.8	3.8						
	Loblolly	5.5	2.6	4.7	4.2	3.4	3.3	2.6	6.1	1.7	2.3				
	S + L	4.3	2.7	4.6	4.8	3.6	3.1	2.7	5.0	1.2	1.7				
												ns	**	ns	ns
304	Slash	3.2	2.8	4.9	5.6	3.7	2.8	3.0	4.1						
	Loblolly	5.3	2.7	4.8	4.3	3.4	3.3	2.9	6.3	1.5	2.1				
	S + L	4.2	2.7	4.9	5.0	3.5	3.1	2.9	5.2	0.8	1.1				
												ns	**	ns	*
335	Slash	3.5	3.1	8.2	9.7	4.7	3.2	3.7	6.9						
	Loblolly	6.2	3.6	10.4	9.9	4.9	4.5	4.3	12.2	2.1	2.9				
	S + L	4.9	3.4	9.3	9.8	4.8	3.8	4.0	9.5	1.7	2.3				
												*	**	**	*
369	Slash	3.6	3.3	9.4	11.5	5.2	3.4	4.1	7.8						
	Loblolly	6.3	4.2	13.5	13.3	5.6	5.3	5.2	14.3	2.3	3.2				
	S + L	4.9	3.8	11.5	12.4	5.4	4.4	4.7	11.1	2.0	2.7				
												*	**	**	*
398	Slash	3.8	3.6	11.1	13.7	5.5	3.7	4.7	9.0						
	Loblolly	6.7	5.1	15.8	16.1	6.3	5.7	6.2	16.5	2.7	3.7				
	S + L	5.2	4.3	13.5	14.9	5.9	4.7	5.4	12.8	2.6	3.6				
												*	**	**	*
431	Slash	4.0	3.9	12.9	16.1	5.7	3.8	4.9	10.6						
	Loblolly	7.1	5.5	18.2	18.6	6.8	6.0	6.7	18.8	2.2	3.0				
	S + L	5.6	4.7	15.5	17.3	6.2	4.9	5.8	14.7	2.8	3.8				
												*	**	**	*
459	Slash	4.1	3.9	13.4	17.2	5.8	3.9	4.9	11.5						
	Loblolly	7.1	5.7	19.5	19.9	6.9	6.1	6.7	19.6	4.2	5.8				
	S + L	5.6	4.8	16.4	18.6	6.3	5.0	5.8	15.6	2.9	4.0				
												*	**	**	*
489	Slash	4.4	4.0	14.5	18.1	5.9	4.1	5.1	12.1						
	Loblolly	8.9	5.9	20.2	21.0	7.0	6.5	6.8	19.9	3.6	4.9				
	S + L	6.7	5.0	17.4	19.5	6.5	5.3	5.9	16.0	2.3	3.1				
												**	**	**	ns
518	Slash	4.8	4.2	15.2	18.7	6.3	4.3	5.6	12.6						
	Loblolly	9.2	6.0	20.7	21.5	7.4	6.8	7.1	20.1	3.4	4.6				
	S + L	7.0	5.1	18.0	20.1	6.9	5.5	6.4	16.3	3.4	4.7				
												*	**	**	ns
550	Slash	4.8	4.4	15.6	19.7	6.4	4.6	6.3	13.0						
	Loblolly	9.6	6.2	21.2	21.8	7.5	6.9	7.3	20.4	3.2	4.4				
	S + L	7.2	5.3	18.4	20.8	6.9	5.7	6.8	16.7	3.6	5.0				
												*	**	**	ns

[1]LSD = Least Significant Difference at the respective levels for recording statistical variance between any two figures in the line, or lines, for which the LSD's are given. One asterisk indicates 5 percent level and two asterisks indicate 1 percent level.

since critical drouth conditions did not need to be overcome, as was the case the first year. If the first year had been normal, it is doubtful that check plot growth would have been superior to the ±0 treatments. Firm seedling establishment during the first year, moreover, enabled satisfactory growth despite excess water the second year.

The pretreatment first-year drouth left soil moisture depleted to the degree that abundant rainfall could be absorbed and retained by the soil without a serious flood condition occurring on the check plots.

FIGURE 5. *An 8-inch plot, showing loblolly pines at the end of the second growing season (left), and a +4-inch plot with hydrophytic vegetation and stunted seedlings (right).*

Also, adequate rainfall well distributed during the growing season favorably influenced survival and growth. If the particular season sampled had been normal, this might imply that for loblolly pine no drainage is needed other than the elimination of permanent ponding. However, average growth on plots with water at −8 inches and −4 inches was almost as much as for the check early in the second

TABLE 3. Survival and growth of seedlings with eight-inch water level treatments in the supplementary study on water-logged soil. Growth calculations (inches) are cumulative with time for surviving seedlings. Survival percentages are based upon trees living at the begining of treatment.

	2-week treatment				4-week treatment				8-week treatment			
	Slash		Loblolly		Slash		Loblolly		Slash		Loblolly	
	Sur.	Gr.	Sur.	Gr.	Sur.	Gr.	Sur.	Gr.	Sur.	Gr.	Sur.	Gr.
	Percent	*Inches*	*Percent*	*Inches*	*Percent*	*Inches*	*Percent*	*Inches*	*Percent*	*Inches*	*Percent*	*Inches*
End of treatment	95	0.4	100	0.4	51	1.2	96	0.9	39	2.9	53	1.9
End of treatment plus 6 weeks	77	2.1	70	1.3	31	2.1	23	1.2	29	3.4	24	2.3
End of treatment plus 12 weeks	76	2.6	61	1.6	31	2.3	21	1.2	29	3.5	22	2.3
End of treatment plus 18 weeks	76	2.7	60	1.7	31	3.1	21	1.7	29	3.6	21	2.3

growing season (335 days), and these three treatments were significantly better (1 percent level) than all others.

Slash pine seedlings, in contrast, had their greatest growth during the entire experiment on −8 plots, although this was not significantly greater than for the −4 treatment. It was, however, significantly more (5 percent level) than on the check plots. Slash pine growth on the check plot was at an intermediate level among all treatments. As stated previously, the variation between species was probably due to the initial difference in the size and apparent vigor of the stock, the loblolly pine being much superior. This, of course, does not account for the disappearance of significance during the period from 166 to 304 days after treatments began.

Growth was slightly better for both species on +4 plots than on the ±0. While slash pine growth on −8 plots was slightly superior to loblolly pine the first year, the opposite occurred the second year. The better growth of loblolly pine than slash pine on the drained plots may indicate that the former is benefited most by drainage in the seedling stage or, again, the larger stock may have been responsible.

Another trend for both species under the coefficient treatments was towards higher average growth with the slowest drainage rate of ⅛-inch per day, though the differences were not significant at any time during the experiment. A coefficient of ⅛-inch is lower than that now used by drainage engineers.

Different water treatments appear to have had little effect on the duration of dormancy. A small amount of growth occurred in January, virtually none in February, and some in March. April was the period of spring flush, and through July of the second year, rapid growth continued on check plots and for −4 and −8 treatments.

In the supplementary study, average growth of slash pine was greater than for loblolly pine at every period of measurement after plots were drained (Table 3). Both species averaged 7.2 inches in height at time of treatment on June 6. This was approximately 0.8 inch less than the depth of flooding. During each period of submergence, growth of surviving slash pine seedlings was equal to, or greater than, that of loblolly pine (Fig. 3).

Temperatures. High survival rate on one +8 plot the first year may have been due to its lower water temperatures. This plot also had abnormally favorable height growth, judging from the growth of seedlings in its replicates. Therefore, detailed temperature measurements were made about every three days during the second growing season to confirm the results from limited data collected the first year. Should further testing substantiate that pines are so sensitive to water temperatures, a practical aspect would be the greater need for elimination of ponding in open fields than where partial shade occurs.

Water temperatures were usually about 2° to 5°F warmer than the air, but on occasion differences of 13°F were recorded. Prior to October, only for the single plot mentioned above was the water temperature cooler than the air, the difference averaging 4°F. During October and November, ambient temperature generally exceeded water temperature. Temperature in the air above flooded plots varied as much as 7°F while water temperatures differed as much as 11°F (Fig. 6). No reason is surmised for these differences during the first year of treatment other than the effect of some shading from a woodland on the west and a shrub hedge to the east of the plots. The temperature variation between plots continued through 1958, and again water temperatures tended to be higher than air temperatures.

Oxygen. Dissolved oxygen in the water of the +8 treatments, as well as in the comparison samples, was extremely inconsistent. In the flooded plots, it ranged from 2.8 to 8.3 mg per liter. Stagnant

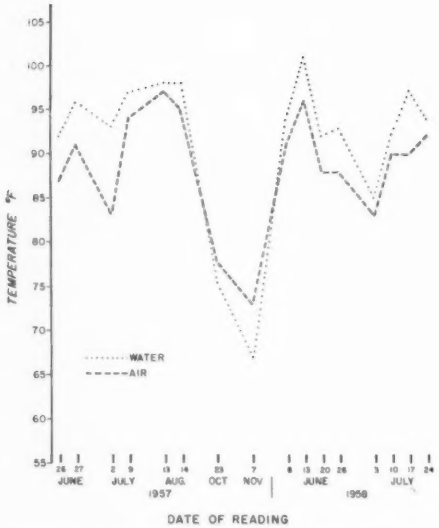


FIGURE 6. *Average air and water temperatures of plots flooded to depths of four and eight inches.*

ponds with timber contained about 5 mg, ponds in the open 7 mg, running streams 7 mg, and the artesian water source ranged from 3.7 to 8.3 mg at the outlet. While poor aeration may have limited growth in the flooded plots, the amount of free oxygen present generally exceeded the requirements for growing plants hydroponically.

Summary and Conclusions

Slash and loblolly pine seedlings planted in a plastic clay loam soil were continuously flooded to ±0, 4, and 8-inch depths; continuously drained to 4 and 8 inches below ground level; and flooded to a depth of three inches at 3-week intervals with subsequent drainage at ⅛, ¼, and ½-inch per day coefficients.

A supplemental study tested survival ability of slash and loblolly pine seedlings planted on waterlogged soil immediately after drainage, but subjected to subsequent 2-, 4-, and 8-week periods of inundation to 8 inches.

Results and suggested practical conclusions are:

1. Mortality was inversely related to height of seedlings. Moreover, it appears that terminal buds must be above water to survive more than a few weeks of inundation.

2. Slash pine seedlings in the plots began to die 68 days after initiation of flooding to 8-inch depths, and loblolly pine within 133 days. Flooding to 8-inch depths resulted in severe mortality, while flooding to 4-inch depths caused significant losses the first year. Slash pine inundated for periods longer than two months and loblolly pine for four months will probably require replanting.

3. One-year-old seedlings of slash and loblolly pine averaging 7.2 inches tall endured a maximum of 2 weeks under 8 inches of water without excessive mortality in the supplemental study. To permit seedling survival, previously water-logged sites, now drained, will require surveillance to guard against prolonged subsequent inundation to depths of 8 inches and over.

4. First year height growth of loblolly pine on plots continuously drained to 4 and 8 inches below ground level considerably exceeded growth where water constants were maintained at ground level and at 4 and 8 inches above that point. Best growth of slash pine was on plots with drainage to a depth of 8 inches, although it was not significantly different than for a 4-inch depth. By the end of the second year, greatest growth for both species was on the plots drained to 8 inches below ground level. Maintaining ground water at a depth of 4 inches, however, appears satisfactory for young seedlings.

5. Among drainage coefficient plots, no real differences occurred between rates of water removal of ⅛, ¼, and ½ inch per day. One-eighth inch coefficients appear satisfactory for seedling establishment.

6. Growth of slash pine exceeded that of loblolly pine following drainage of all plots inundated from 2 to 8 weeks, indicating a greater ability of the former to

withstand unfavorable water conditions.

7. Trees in several plots grew twice as much from October 11 to November 13 as in the 133 days prior to October 11.

Literature Cited

AHLGREN, C. E., and H. L. HANSEN. 1957. Some effects of temporary flooding on coniferous trees. J. For. 55: 647-650.

BERGMAN, H. F. 1920. The relation of aeration to the growth and activity of roots and its influence on the ecesis of plants in swamps. Ann. Bot. 34: 13-33.

DEAN, B. ELIZABETH. 1933. Effect of soil type and aeration upon root systems of certain aquatic plants. Plant Physiol. 8: 203-222.

DEMAREE, DELZIE. 1932. Submerging experiments with Taxodium. Ecol. 13: 258-262.

GREEN, W. E. 1947. Effect of water impoundment on tree mortality and growth. J. For. 45: 118-120.

HUNT, F. M. 1951. Effect of flooded soil on growth of pine seedlings. Plant Physiol. 26: 363-368.

JACKSON, W. T. 1956. The relative importance of factors causing injury to shoots of flooded tomato plants. Amer. J. Bot. 43: 637-639.

KOZLOWSKI, T. T. 1958. Water relations and growth of trees. J. For. 56: 498-502.

KRAMER, P. J. 1933. The intake of water through dead root systems and its relation to the problem of absorption by transpiring plants. Amer. J. Bot. 20: 481-492.

————. 1949. Plant and Soil Water Relationships. McGraw-Hill Book Co., N. Y. pp. 150, 220 *et. fol.*

————. 1951. Causes of injury to plants resulting from flooding of the soil. Plant Physiol. 26: 722-736.

KUSTER, A. 1948. Der Einfluss der Juraseen-Hochwasser auf die Strandwaldungen. Schweiz. Z. Forstw. 99: 428-438.

LEYTON, L., and L. Z. ROUSSEAU. 1958. Root growth of tree seedlings in relation to aeration. *In* The Physiology of Forest Trees. Ronald Press, N. Y.

PARKER, J. 1950. The effects of flooding on the transpiration and survival of some southeastern forest tree species. Plant Physiol. 25: 453-460.

PRUITT, A. A. 1947. Study of effects of soils, water table, and drainage on the height growth of slash and loblolly pine plantations on the Hoffmann Forest. J. For. 45: 836.

SATTERLUND, D. R., and S. A. GRAHAM. 1957. Effect of Drainage on Tree Growth in Stagnant Bogs. Mich. For. No. 19. U. Mich., Ann Arbor.

SCHLAUDT, E. A. 1955. Drainage in forestry management in the South. *In* Water. Yrbk. of Agric., U. S. Dept. Agric.

SCOTT, A. D., and D. D. EVANS. 1955. Dissolved oxygen in saturated soil. Soil Sci. Soc. Amer. Proc. 19: 7-12.

SOLVAY CO. 1957. Water Analysis. Technical and Engineering Service Bull. 11.

STONE, E. L., R. R. MORROW, and D. S. WELCH. 1954. A malady of red pine on poorly drained sites. J. For. 52: 104-113.

TROUSDELL, K. B., and M. D. HOOVER. 1955. A change in groundwater level after clearcutting of loblolly pine in the Coastal Plain. J. For. 53: 493-498.

YEAGER, L. E. 1949. Effect of Permanent Flooding in a River Bottom Timber Area. Ill. Nat. Hist. Surv. Bull. 25, Art. 2.

Seasonal Variation in the Moisture Content of the Green Leaves of Mountain Laurel

BY
WILLIAM E. REIFSNYDER

THE MOISTURE CONTENT of forest fuels is a major factor influencing the flammability of the forest fuel complex. Changes in moisture content exert a powerful and often controlling influence on fire behavior. Since most fires burn primarily in the dead fuels, it is understandable that fire control personnel have been concerned almost solely with moisture content of the dead fuels. But live vegetation is also a factor in determining how a fire behaves. As a fire becomes more intense, more and more of the green understory vegetation becomes involved. Thus the moisture content of understory vegetation may exert a controlling influence on fire intensity and may determine whether or not a fire will pass from a surface fire to a crown fire.

Little is known of how the moisture content of green leaves varies with time through a fire season or a year. Unanswered or partially answered questions include these: How does the moisture content of new growth compare with the older leaves on evergreen species? How does dryness of site affect the moisture content of leaves? Are green leaves drier in dry years than in wet years?

The present study was established to attempt to answer these questions for mountain laurel (*Kalmia latifolia* L.), an evergreen shrub common in the northeastern states.

Mountain laurel is an understory shrub growing in dense thickets in the hardwood forests of the Northeast. As a forest fuel type, it is classed as *extreme* in the rate of spread classification developed by Jemison and Keetch (1942).

Previous Work

Studies of seasonal variation in moisture content of evergreen shrubs have been carried out primarily in western forests and in Europe. New leaves of brush species of *Arctostaphylos*, *Ceanothus*, *Adenostoma*, and *Quercus*, growing in California and Idaho, contained moisture contents usually above 200 percent of their dry weight at the beginning of the growing season (Firestop 1955, Richard 1940, Buck,[1, 2] and Fons[3]). But moisture contents decreased

[1]Buck, C. C. Progress report on variations in the moisture content of green brush foliage on the Shasta Experimental Forest during 1937. Calif. For. and Range Expt. Sta. unpub. mss. 1938.

[2]Buck, C. C. Progress report on variations in the moisture content of green brush foliage on the Shasta Experimental Forest during 1938. Calif. For. and Range Expt. Sta. unpub. mss. 1939.

[3]Fons, W. L. Progress report on seasonal variations in moisture content of chaparral on the San Dimas Experimental Forest during 1942. Calif. For. and Range Expt. Sta. unpub. mss. 1943.

The author is on the faculty of the Yale Forestry School, Yale University, New Haven, Conn. He wishes to thank George M. Furnival for advice on statistical techniques. Manuscript received Jan. 11, 1960.

rapidly through the summer, reaching minimum values of 65 to 120 percent in the fall, usually in September. Thereafter, leaf moisture increased slowly to a level of about 100 percent in the winter and spring.

These same studies showed that the old leaves of the same species reached a minimum moisture content in the late winter or spring, at values between 75 percent and 100 percent. As the new flush of growth occurred, the old leaves also increased their moisture content, reaching a maximum of about 120 percent in the summer, then decreasing to 100 percent or less in the fall. There often followed a winter increase, with a second minimum in the spring just before the new growth appeared.

Measurements on *Rhododendron ferrugineum*, *Calluna vulgaris*, and *Arctostaphylos uva-ursi* in Europe (Ulmer 1936) showed a similar cycle of leaf moisture content.

Design and Procedures

An even-aged oak forest of sprout origin with an abundance of mountain laurel in the understory was chosen as the experimental area. The oak stand, approximately 57 years old at the time of the study, occupied the east-facing slope of West Rock Ridge, just above a small reservoir, Lake Wintergreen. The area, wholly within the Eli Whitney Forest, and just outside the northwest boundary of the city of New Haven, Connecticut, has been described in detail by Chapman.[4]

Three areas containing a heavy undergrowth of laurel and which appeared likely to have widely different soil moisture conditions were selected. One was on the flat at the bottom of the ridge, near the reservoir; this is referred to as the "bottom" site. Another, the "midslope" site, was about 400 feet distant on a gentle slope. The third, another 400 feet up the slope, on a rocky knoll with very shallow soil about 50 feet above the level of the reservoir, is referred to as the "knoll" site.

Leaf samples were taken at irregular intervals from March 1957, through November 1958, more frequently during spring and summer months than during fall and winter. Separate samples were taken from two clumps of bushes 25 to 100 feet apart on each of the areas, and leaves were collected from various levels on the plants. Collections were made from different plants each time, in order not to defoliate any one plant. New leaves were collected and analyzed separately from old leaves as long as it was possible to distinguish them by their color and feel, and as long as analysis showed that their moisture contents differed measurably.

Collections were made in early afternoon, as close to 2:00 pm as possible, in order to obtain leaves when they could be expected to have the lowest moisture content of the day. Systematic bias was eliminated as much as possible by varying the sequence in which collections were made. Total time for collecton was about one-half hour. Collections were not made on the day of a rain, and care was taken to see that no leaves were taken that had obvious surface moisture.

The samples, each of which consisted of approximately 40 grams of leaves, were analyzed for moisture content by the xylene distillation method described by Buck and Hughes (1939).

In order to study possible effects of soil moisture on leaf moisture content, a running soil moisture budget was maintained for the period of the study. Inasmuch as the main purpose of the soil moisture budget was to enable rough comparisons between the two years of the study, it was not considered essential to have absolute soil moisture values.

Accordingly, a climatological method was selected which maintained the budget in terms of potential evapotranspiration and rainfall. Although numerous such methods

[4]Chapman, G. L. The influence of mountain laurel undergrowth on environmental conditions and oak reproduction. Yale School of Forestry, Ph.D. dissertation. 157 pp. 1950.

have been developed, I used the one developed by Hamon (Travelers Weather Research Center, 1957), which has given good results in Connecticut.

The soil was considered to be at field capacity at the end of the winter, on April 1. For each day, estimated evapotranspiration was subtracted and the rainfall amount added to the budget. In Hamon's method, potential evapotranspiration is considered to be a function of day length and the difference in water vapor density at daily maximum and minimum temperatures. Following Palmer and Havens (1958), I reduced computed potential evapotranspiration values by the same percentage as the previous day's soil moisture percent to gain an estimate of actual evapotranspiration. It was considered that field capacity of the soil at all three locations was two inches of water. The assumption of constant field capacity had the effect of diminishing possible estimated differences between years on the dry sites as compared with the areas with deeper soil. This was not considered serious inasmuch as the two years showed marked differences in estimated soil moisture and the use of different field capacities for the three areas would have had the effect only of emphasizing these differences on the shallower soils.

Rainfall amounts used in the soil moisture budget calculations were estimated from precipitation recorded at three nearby stations: Mt. Carmel (4½ miles); New Haven Airport (7¾ miles); and Lake Dawson (¾ mile). Despite the closeness of the Lake Dawson guage, it was not used alone because it was on the opposite side of the ridge from the experimental area. Weighted averages were calculated, using weighting factors inversely proportional to the distances of the several weather stations from the experimental area.

Maximum and minimum temperatures used in computing the budget were those recorded at Mt. Carmel, the nearest temperature station in a similar topographic position. Rainfall and temperature data were taken from *Climatological data, New England* (U. S. Weather Bureau, 1957 and 1958).

Results

Individual moisture content values of the laurel leaves are contained in Table 1. The data are plotted in Figure 1, along with soil moisture values expressed as a percent of assumed field capacity. Each knoll site point is an average of two samples. These are labelled "dry site" in the figure. Other points are averages of four samples, as explained in the next section, and are labelled "moist site" in the figure.

Analysis

In order to test the hypothesis that there were no differences between the three areas, an analysis of variance was performed on the old-growth leaves (Table 2). Duncan's (1955) test for the significance of differences in ordered means showed that the difference between means of the bottom and midslope sites was not significant, whereas the knoll mean was significantly different from both of the others. Accordingly, data from the two lower sites were grouped. In Figure 1, these data are labelled "moist site."

The analysis also disclosed that there was significant variation with time, a conclusion that is evident from inspection of the graph. The non-significant interaction can be interpreted as indicating that the three sites behaved similarly throughout the year.

A similar analysis performed on the new growth leaves (Table 3) yielded the same conclusions. In this case, the rapid decrease of moisture content as the leaves matured contributed to the large mean square for time.

The year 1957 was one of extreme agricultural drought in Connecticut. Hamon's analysis (cited previously) showed that, ". . . the drought of 1957 was more severe than any combination of the driest growing seasons during the past 30 years." The following year, 1958, on the other

TABLE 1. Moisture content of laurel leaves in percent of dry weight.[1]

Date collected	Current year's leaves			Old-growth leaves		
	Knoll	Midslope	Bottom	Knoll	Midslope	Bottom
			Percent			
3/29/57				104 132	126 117	129 114
4/12/57				118 116	126 126	122 115
4/19/57				119 114	138 119	136 118
4/26/57				109 110	112 111	120 113
5/ 3/57				106 97	112 97	104 112
5/ 9/57				100 105	121 108	123 110
5/24/57	299 287	351 347	288 301	123 115	133 76	124 121
6/ 7/57	224 192	273 243	260 321	129 124	143 141	144 130
6/18/57	160 166	203 194	218 202	118 132	146 152	153 150
7/10/57	141 140	154 176	156 155	133 113	149 158	154 144
8/ 6/57				136 133	157 150	150 150
8/13/57				108 114	143 142	152 149
8/29/57				128 128	155 146	150 162
9/24/57				141 132	157 155	161 162
10/10/57				137 139	157 141	156 156
11/14/57				130 134	140 134	130 138
2/ 3/58				130 124	130 127	129 124
3/ 7/58				126 128	134 133	130 138
4/ 4/58				131 127	129 134	116 127
4/18/58				121 124	127 126	125 125
4/30/58				118 120	116 111	129 113
5/12/58	170 211	239 227	229 222	100 107	96 103	100 110
5/26/58	269 286	305 291	274 280	98 97	98 99	106 100
6/16/58	213 232	261 237	231 263	121 111	135 128	130 128
7/ 3/58	203 351	204 218	203 230	156 154	170 163	140 174
7/16/58	169 176	179 199	178 177	153 160	160 144	174 151
7/29/58	153 176	191 170	227 175	154 164	161 164	135 164
8/11/58				143 135	171 154	167 166
9/22/58				156 131	154 160	173 154
10/31/58				134 129	140 128	123 144

[1]Two values shown for each category.

hand, had a plentiful supply of precipitation: 52 inches at New Haven, compared with a normal of 46 inches. This fortuitous circumstance gave an excellent opportunity to assess the effect of two greatly different moisture regimes on leaf moisture content. It should be pointed out, however, that although the 1957 summer was very dry for southern New England, it cannot be compared with the typical long dry season experienced on the West Coast of the United States.

In order to test the hypothesis that there was no correlation between soil moisture differences and leaf moisture differences between the two years, the following procedure was used. Monthly averages of the laurel leaf moisture content were computed for the knoll site and for all sites grouped. Values for 1958 months were then subtracted from the corresponding 1957 months to give a series of differences. A similar series of differences was calculated from soil moisture values. These differences are compared in Table 4. From an inspection of the soil moisture values, it is evident that 1957 was indeed a drier year than 1958, at least during the months of March through July, confirming Hamon's work cited earlier.

The apparent lack of correlation between soil and leaf moisture is confirmed by regression analyses of leaf moisture on soil moisture which yielded correlation coefficients of 0.21 and 0.08, neither of which is significant at the 5 percent level. It may be argued that calendar months are not the appropriate time divisions inasmuch as

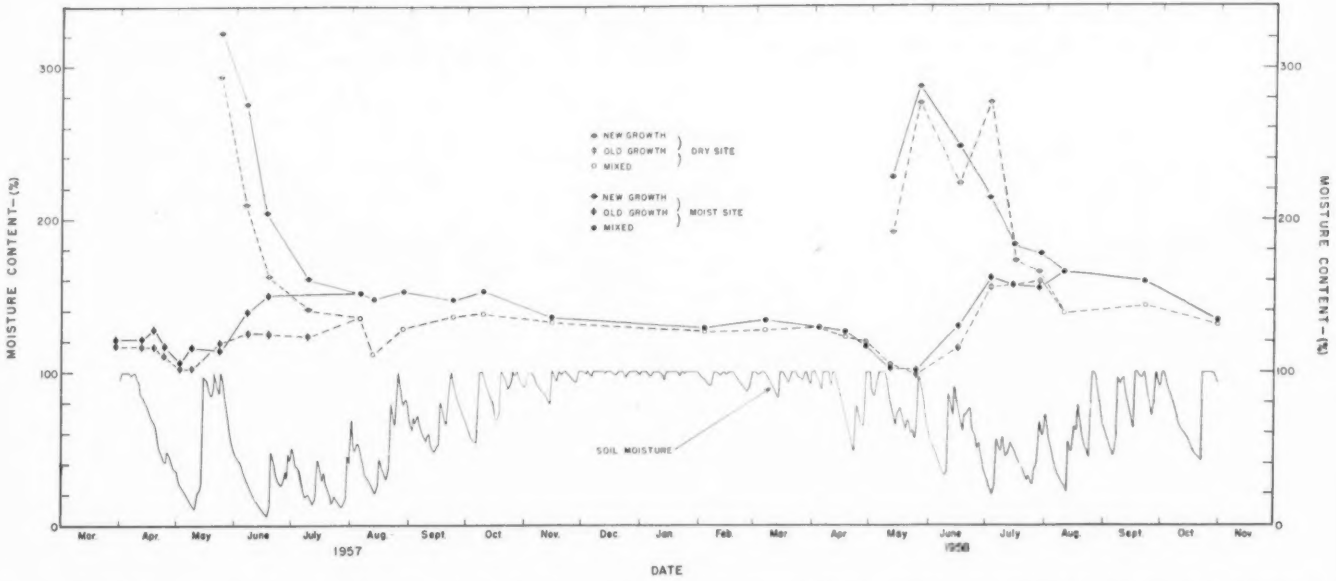


FIGURE 1. *Moisture content of soil and laurel leaves. Leaf moisture is expressed in percent of dry weight; soil moisture, in percent of field capacity*

TABLE 2. Analysis of variance of old-growth laurel leaves.

Source of variation	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Time	29	52,156	1,798	23.57**
Site	2	3,824	1,912	25.07**
T × S	58	5,746	99.1	1.30
Error	90	6,864	76.3	
Total	179	68,590		

**Significant at 1 percent level.
Site means: Knoll—125.5 percent; midslope—134.7 percent; bottom—135.8 percent.

TABLE 3. Analysis of variance of new-growth laurel leaves.

Source of variation	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Time	9	134,395	14,933	23.49**
Site	2	5,678	2,839	4.47*
T × S	18	18,807	1,045	1.64
Error	30	19,071	636	
Total	59	177,951		

*Significant at 5 percent level.
**Significant at 1 percent level.
Site means: Knoll—140.6 percent; midslope—155.4 percent; bottom—153.0 percent.

plants are influenced in their growth by factors other than the calendar. However, growth stages in these two years did not differ by more than about two weeks. In contrast to this, the period of drought lasted five months. Furthermore, since the drought was a severe one for the southern New England region, any important leaf moisture differences would be expected to show up even when analyzed on a monthly basis.

Surprisingly, and contrary to expectations, moisture content of laurel leaves was high in the driest months, May and June 1957, as compared with the same months in 1958. This contrasted with soil moisture, which was low during May and June 1957 as compared with the same months in 1958.

A further attempt was made to correlate leaf moisture content with potential evapotranspiration calculated for the day in which the sample was collected. These calculations, which are not shown, also failed to demonstrate a relationship between leaf moisture and drying power.

TABLE 4. Comparison of leaf and soil moisture contents for a dry year and a wet year. (1957 value minus 1958 value).

Month	Average soil moisture (percent)	Average laurel leaf moisture content	
		Dry site (percent)	All sites (percent)
Mar.	— 4	— 9	—12
Apr.	—12	—10	— 4
May	—24	8	8
June	—31	10	12
July	—16	—34	—16
Aug.	5	—15	—14
Sept.	—11	— 8	— 4
Oct.	8	6	15
Correl. coefficients[1]		0.21	0.08
Value for significance at 5 percent level		0.63	0.63

[1]Coefficients of correlation between leaf moisture differences and soil moisture differences.

Although it is contrary to common sense and expectation, there appears to be no evidence in these data that there is a relationship between laurel leaf moisture and the dryness of the year. This is especially surprising in view of the fact that there apparently is a leaf-moisture difference between plants growing on a rocky area and nearby plants growing on an area with deeper soils and presumably a greater moisture supply. It may be that plants on the rocky area have undergone some physiological conditioning or even a genetic change which is reflected in lower average leaf moisture contents as compared with nearby plants on better-watered areas. This internal conditioning may be powerful enough to mask year-to-year variations, at least with the moisture conditions prevailing in southern New England.

It seems unlikely that there was no moisture stress on these plants inasmuch as agricultural plants throughout the area on much deeper soils did exhibit serious drought symptoms. However, and this may be important, the moisture stress on these understory laurel plants may be much less than the overstory vegetation because there is very much less net radiation available for evapotranspiration under the shade of the overstory. There is no reason to believe that the plants on the rocky area had any hidden moisture supply although it is possible that the plants on the lowest site were able to tap water from some depth. This seems unlikely, however, in view of the fact that all three sites responded similarly as indicated by the non-significant time-x-site interaction. It would certainly be unwise to make generalizations on the basis of this one example. However, the relationships (or lack of them) revealed in this study are sufficiently unorthodox to warrant further study.

Conclusions

The following specific conclusions may be drawn from the study:

1. Green laurel leaves from plants growing on the rocky, shallow soil site were consistently drier than those growing in deeper soils. The differential was about 15 percentage points, greater in summer, less in winter and early spring.

2. Old-growth laurel leaves varied in moisture content cyclically throughout the study period, reaching minimum values in May and maximum values in late summer. During the two years of measurements, moisture content of laurel leaves was about 100 percent during the spring fire season and about 140 percent during the fall fire season.

3. No clear relationships between drought and leaf moisture content could be demonstrated. Visual inspection of the graphs of old-growth leaves seems to indicate slightly lower moisture contents in the dry year, but the differences do not stand up under statistical analysis. It should be remembered that 1957 was an extraordinarily dry year for Connecticut (although much wetter than a typical California summer) whereas 1958 was well watered, with more than normal rainfall.

4. New leaves of laurel started with a moisture content of about 300 percent, at least when they were large enough and numerous enough to collect. Their moisture content decreased steadily, approaching that of the previous year's leaves asymptotically, reaching old-leaf values in about two month's time.

Literature Cited

Buck, C. C. and J. E. Hughes. 1939. The solvent distillation method for determining the moisture content of forest litter. J. For. 37:645-651.

Duncan, David B. 1955. Multiple range and multiple *F* tests. Biometrics 2(1): 1-42.

Firestop. 1955. Seasonal changes in chaparral moisture. Progress Rep. No. 6. 7 pp.

Jemison, G. M. and J. J. Keetch. 1942. Rate of spread of fire and its resistance to control in the fuel types of eastern mountain forests. Appalachian For. Exp. Sta. Tech. Note 52. 15 pp.

PALMER, WAYNE G. and A. V. HAVENS. 1958. A graphical technique for determining evapotranspiration by the Thornthwaite method. Mon. Weather Rev. 86(4):123-128.

RICHARDS, L. W. 1940. Effect of certain chemical attributes of vegetation on forest inflammability. J. Agric. Res. 60(12):833-838.

TRAVELERS WEATHER RESEARCH CENTER. 1957. Analysis of the agricultural drought in Connecticut during 1957. Part II. Travelers Weather Res. Center. 7 pp.

ULMER, WALTER. 1936. Über den Jahresgang der Frosthärte einiger immergrüner Arten der Alpinen Stufe, sowie der Zirbe und Fichte. Unter Berücksichtigung von osmotischem Wert, Zuckerspiegel und Wassergehalt. Jahrb. f. wiss. Bot. 84:553-592.

U. S. WEATHER BUREAU. 1957. Climatic data, New England. Vol. 69. (also Vol. 70, 1958).

Forest Fertilization

Forstdüngung. By Detlev Brüning. Neumann Verlag. Leipzig. 210 pp. 1959. 18.00 E. German Marks. (German with Russian and English summaries).

Review by Albert L. Leaf
State University College of Forestry
At Syracuse University, Syracuse, New York

Recently from East Germany has come a new publication on fertilizing forests. This book, with an introduction by Professor W. Erteld and a foreword by Professor W. Wittich, discusses the effect of potash and magnesium additions on the development of *Pinus sylvestris*, *Robinia pseudoacacia*, and *Quercus borealis*. The three major sections of the book deal with (1) experiments with Scotch pine in the region of Templin, (2) experiments with black locust, red oak and Scotch pine in the Schreen forest district, and (3) investigations concerned with the phenomena and appearances of nutrient deficiencies in the three tree species.

In addition to discussing growth of vegetative responses of the investigated species growing on degraded sandy soils, poor in nutrients and influenced by subsoil water, there is also a discussion of generative development of black locust. Mentioned are the effects of potash-magnesia fertilization on flowering, frost resistance, defoliation, depth of root penetration, abundance of root nodules and quantities of nitrogen, and resistance to brown scale (*Eulecanium corni*) of black locust; also the effect of rabbit and hare damage on red oak as influenced by fertilization.

Because of the limited number of reports on potassium and magnesium fertilizer responses in forestry, this book is a real contribution to the literature. It substantiates previous work that potassium and magnesium fertilization must be considered in the amelioration of depleted sandy sites.

The book contains numerous tables, charts and photographs. Of special note are the 33 pages of excellent color photograph plates depicting nutrient deficiencies and growth responses obtained as well as profiles of soils supporting the nutrient-deficient trees. There are 138 literature citations.

With its high standards of preparation, illustration, typography and paper, the book will be of great value and interest to those concerned with forest fertilization and tree nutrition.

Vegetative Indicators of Rate of Height Growth in Ponderosa Pine

BY
R. DAUBENMIRE

DURING the course of a study aimed at delimiting the basic categories of forest vegetation of eastern Washington and northern Idaho, the writer noted what appeared to be consistent differences in the rate of height growth of ponderosa pine (*Pinus ponderosa* Laws.) as it occurs naturally in different habitat types.[1] As that study neared completion, the U. S. Forest Service, through the helpful cooperation of Charles A. Wellner and Donald W. Lynch, made available height and age determinations of a series of *P. ponderosa* stands that had been studied in connection with silvicultural research. When these stands were revisited and classified by the writer according to habitat types, the existence of a correlation with growth was confirmed, but it was so weak that plant communities seemed to have little value for predicting growth rate of the pine.

In this preliminary study the basic height and age data for the different stands were extrapolated to a common stand age of 100 years (the site index), using data from a table presented by Meyer (1938) which had been offered for this purpose. If such data should not accurately reflect the growth rate of a tree at different ages, then the extrapolated height at 100 years would be proportionately inaccurate. With this thought in mind the writer subsequently tried plotting directly the raw meaurements of height and age, keeping the data for different habitat types on separate scattergrams. When this was done rather sharp differences among certain of the habitat types were revealed. Thus encouraged, the writer began to study additional stands so as to show the extent of differences in potentialities among the habitats more adequately, and to investigate the reason why the site index method is inferior to the use of raw data.

Methods

Since the Forest Service data were not obtained with the idea of sampling equally all the seven habitat types in which *P. ponderosa* may be found abundantly in eastern Washington and northern Idaho (Daubenmire 1952), it was necessary to expand the initial nucleus of data so that all habitats were adequately represented. Stands

[1] A habitat type (syn.: homoece, equivalent environment) is all the area that supports, or is capable of supporting, the same kind of climax vegetation in the absence of disturbance by fire, logging, heavy grazing, etc. Each habitat type will be referred to by the name of the climax plant association that characterizes it, and the abbreviation h.t. will be used freely.

The author is on the faculty of Washington State University, Pullman.

In addition to the cooperation of the U. S. Forest Service and T. S. Russell mentioned in the text of this report, Jean B. Daubenmire shared in most of the field work. A part of the field expenses were met with funds provided for biological and medical research by Washington State Initiative 171. Valuable suggestions for improving the manuscript were made by D. W. Lynch. Manuscript received Feb. 27, 1960.

abnormally open or extremely dense were avoided, and the height of at least five trees in or projecting slightly above the main canopy was measured with an Abney level. Age was assumed to equal the number of wood layers counted on borings made at breast height, plus ten as an estimate of the time required for the seedling to have attained this height. It would have been better to have used a larger figure for age at breast height for trees growing slowly on poor sites, and a smaller figure for good sites, but in a study to distinguish poor from good sites this would hardly be an objective procedure without more evidence on rates of seedling growth than is now available.

The data were plotted as scattergrams, a separate one for each habitat type. To facilitate visual comparisons the outlines of one scattergram representing relatively rapid growth (*Pinus ponderosa/Symphoricarpos albus* h.t.) and one representing relatively slow growth (*Pinus ponderosa/Agropyron spicatum* h.t.) were then superimposed on each of the other scattergrams (Fig. 1).

Results and Discussion

It was found that the habitat types could be divided into four unequal groups on the basis of rate of height growth of *Pinus ponderosa:*

I. BEST POTENTIALITY

Abies grandis/Pachistima myrsinites h.t.

II. GOOD POTENTIALITY

Pseudotsuga menziesii/Physocarpus malvaceus h.t.

Pinus ponderosa/Physocarpus malvaceus h.t.

Pinus ponderosa/Symphoricarpos albus h.t.

III. FAIR POTENTIALITY

Pseudotsuga menziesii/Calamagrostis rubescens h.t.

IV. LOW POTENTIALITY

Pinus ponderosa/Purshia tridentata h.t.

Pinus ponderosa/Agropyron spicatum h.t.

As pointed out earlier, it seemed necessary for the sake of objectivity to count wood layers at breast height and then to add 10 to account for the years required for the seedling to have grown to this height. Not only does the standard value of 10 mask a tremendous variation, but on unproductive habitats the value should be higher than 10, and vice versa. It is therefore important to note that if seedling as well as older trees grow slowly on poor sites, the use of 10 for both good and poor sites reduces the apparent difference between them. Lynch (1958) estimated the following values as appropriate for the breast-height age:

Site	*Years at breast height*
I	3
II	5
III	7
IV	10
V	14
VI	16

If it may be assumed that his Site IV is roughly equivalent to the *Pinus/Symphoricarpos* h.t. and his Site VI to the *Pinus/Agropyron* h.t., and the vertical positions of the scattergrams compared in Figure 1 are adjusted accordingly, then about half the already small overlap is eliminated.

The study has shown that the growth rate of the pine bears no relation to its successional status, for it grows well as a seral tree on burned or logged parts of the *Pseudotsuga/Physocarpus* h.t., and as a climax tree on *Pinus/Symphoricarpos* and *Pinus/Physocarpus* h.t.

Although available moisture is a very potent factor governing the distribution and physiology (Daubenmire 1943, 1946) of trees in the Rocky Mountain region, site quality is not related to moisture alone The *Pseudotsuga/Calmagrostis* flora is less xero-

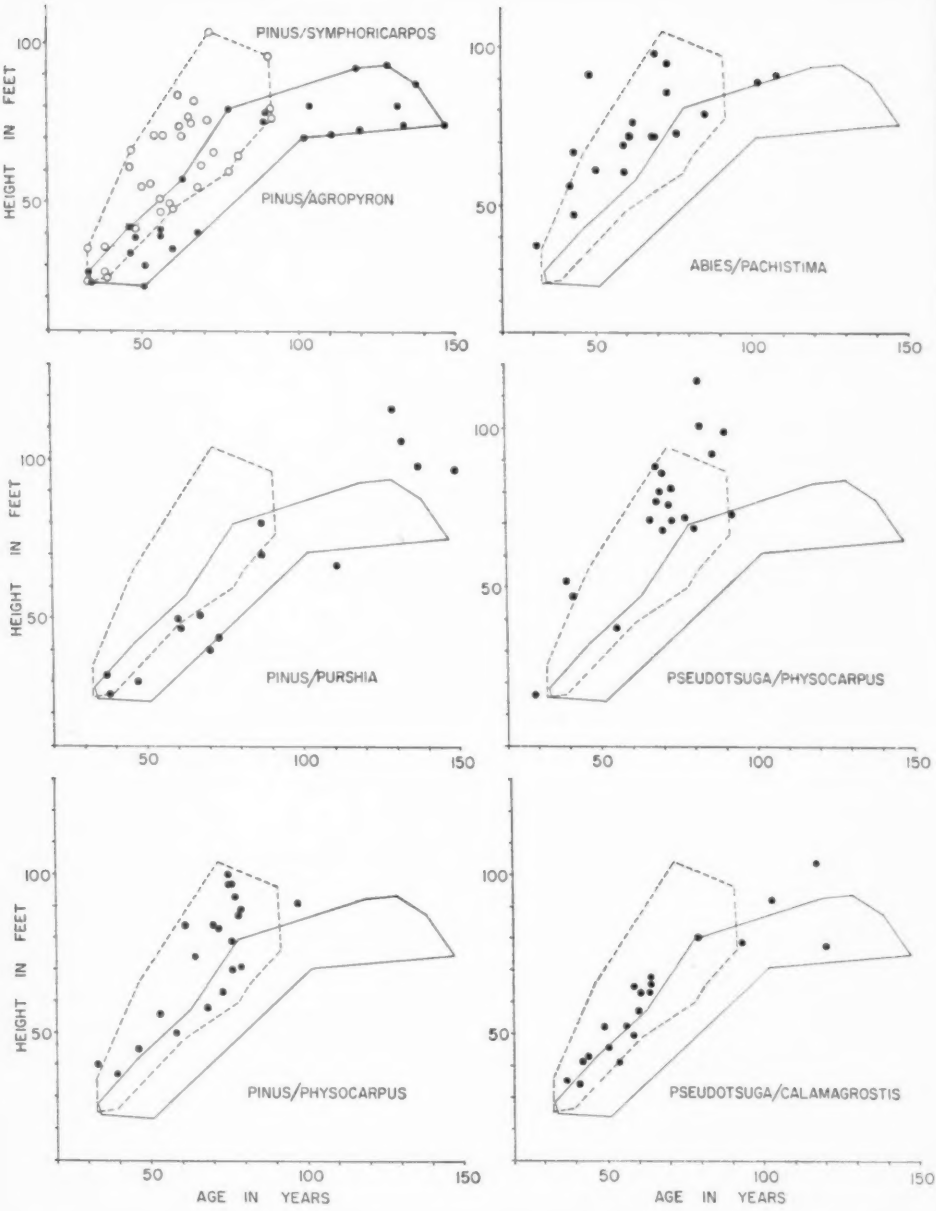


FIGURE 1. *Each point on the scattergrams represents the average height and estimated average age of a group of at least five trees. The gross outlines of the pattern of points for the* Pinus/Symphoricarpos *and* Pinus/Agropyron *habitat types have been superimposed on the data for the others to facilitate visual comparisons. Data for a few stands fall outside the ranges of the values for these ordinates and abcissas and so have been omitted.*

phytic than the *Pinus/Symphoricarpos* and *Pinus/Physocarpus* floras but the growth of the pine is inferior in the first. Since *Pseudotsuga/Calamgrostis* sites are characteristic of coarse glacial till, there is clear indication that lack of fertility more than offsets the superior water relations of this habitat type.

The *Pseudotsuga/Calamagrostis* habitat type as represented in eastern Washington and northern Idaho always has a fair amount of shrubs belonging to the *Symphoricarpos* and *Physocarpus* unions (see key to habitat types for taxonomic lists), rather than the apparently pure sward of *Calamagrostis* so characteristic of *Pseudotsuga/Calamagrostis* stands in the foothills of the Cascades, in Montana, or in central British Columbia (Tisdale and McLean 1957). Thus the habitat type in eastern Washington and northern Idaho is represented chiefly by intergrades between *Pseudotsuga/Calamagrostis* and *Pseudotsuga/Physcoarpus* h.t. Considering all stands in which *Pseudotsuga* is the sole climax dominant, it was found empirically that if there is a fair amount of *Calamagrostis* present, and the stand is in the glaciated northern half of the study area, the growth rate of the pine is markedly reduced in comparison with sites where this grass is nearly if not completely absent. Therefore the hybrid-type stands containing at least a fair amount of *Calamagrostis* and located on glacial soils are to be kept separate from typical *Pseudotsuga/Physocarpus* stands, whether the latter are on glaciated or unglaciated soils, and from *Pseudotsuga* sites that have a fair amount of *Calamagrostis* but are on unglaciated soils.

South of the glacial border where soils nearly always include an admixture of loess, *Pinus/Agropyron* sites are rare, but northward they are abundant, alternating with *Pinus/Symphoricarpos* growing on what may be interpreted as patches of more favorable soils. In this northerly sector many forests have patches of the two undergrowth types forming a mosaic of small units. It was discovered that even if only a moderate share of the mosaic is represented by the *Symphoricarpos* type of undergrowth, the pine grows as well as if the shrub layer were continuous.

The height of the group of shrubs considered as belonging to the *Symphoricarpos* union varies from about 0.5 to 1.5m, and from recorded estimates of shrub height in many stands an attempt was made to relate this variable to differences in rate of height growth of pine within the *Pinus/Symphoricarpos* h.t. No relationship was found.

Many stands of *Pinus ponderosa* in the area of study are heavily infected with *Arceuthobium campylopodum*, whereas other areas completely lack this pathogen. Before the growth rate study was far along it was discovered that forest undergrowth is closely correlated with susceptibility of the pine to the disease caused by *Arceuthobium*, infection being common on *Pinus/Agropyron* and *Pinus/Purshia* habitat types, but not seen elsewhere. It is interesting to note that Shepherd (1959) found a parallel correlation between the susceptibiilty of *Picea engelmanni* to insect infestation and the character of the forest undergrowth.

Validity of the Standard Site Index Curves

As mentioned earlier, raw data show better correlations between growth rates of *Pinus ponderosa* and habitat types than are obtained after the site index curves have been used to extrapolate to a common age (Table 1). Such a situation casts doubt on the validity of the curves for *P. ponderosa* in eastern Washington and northern Idaho, and calls for testing them in other ways.

The best opportunity for testing was provided at the edges of old burns where several decades ago fire had stopped part way through a pine stand permitting establishment of a new generation of trees adjacent to the older residual stand on what appeared, from considerations of topography, soils and non-arborescent vegetation, to be parts of one homogeneous habitat. If the site index curves are valid, the values for the contiguous young and the

old stands should be closely similar, but among the 11 opportunities to make such a comparison there were errors up to 28 percent in prediction (Table 2). It is to be noted that the older stand always has the higher site index. The evidence thus indicates that the shape of the postulated growth curves is materially different from the actual growth rates of *P. ponderosa* in the region under study. Within the age range studied, growth is more rapid than postulated (See also Fig. 2A). Although these "fire-line" data obtained at the edges of old burns play havoc with the site index curves, they are all included in Figure 1 where they fit harmoniously with other measurements made on the corresponding h.t.

Another manner of testing the validity of the site index curves is to count wood layers of felled trees at different heights along the axis, and construct curves to be compared with those based on mathematical manipulation of height and age data for many stands. Only twice was there opportunity to make this type of an analysis, but the results (Fig. 2A) of both tests are in complete agreement with the results of "fire-line" studies, namely that the pine grows much faster than the site index curves suggest.

TABLE 1. Classification of stands of Pinus/Agropyron *and* Pinus/Symphoricarpos *habitat types according to site index. Note that modal values almost overlap.*

Site index Class	Numbers of stands	
	Pinus/ Agropyron	*Pinus/ Symphoricarpos*
40- 45	1	
46- 50	1	
51- 55	2	
56- 60	2	1
61- 65	5	2
66- 70	5	4
71- 75	3	5
76- 80	2	3
81- 85	3	4
86- 90		1
91- 95	1	2
96-100		4
101-105		3
106-110		1
111-115		1
116-120		
121-125		1
Totals	25	32

One might easily suspect the validity of any site index table that does not rest on an ecologic foundation. It has been firmly established that the species of the taxonomist is usually not an ecologic unit, but rather a mosaic of ecotypes embracing as much heritable variation (in growth rate, for example) as one finds between species. The distinctive combination of climate and soil of each habitat type exerts a distinctive selective pressure on biotypes and hence tends to produce its own ecotype. The clear differences in growth data for the different habitat types may represent such genetic differentiation, or simply ontogenetic modification, or a combination of the two. Tests under controlled conditions have demonstrated that contiguous habitats may support genetically differentiated ecotypes (Daubenmire 1960, McMillan 1956, Bradshaw and Snaydon 1959, Habeck 1958). The site index concept recognizes but one family of harmonic curves representing dozens of distinctive habitat types ranging from South Dakota to the foothills of the Sierras and Cascades, and from the Canadian border to Colorado. Such an expression of growth ignores an important principle of ecology, and it is significant to note that others too have found it impractical to use the same site index curves for contiguous habitats (Carmean 1956, Lorenz and Spaeth 1947).

Spurr (1956) has sounded the extremely important warning that nearly all work done to establish relations between soil profile characters and tree growth has involved passing the raw data through some standard site index manipulation. All such research stands in jeopardy unless the site index curves accurately reflect the growth

TABLE 2. Comparison of site indexes for 11 pairs of stands of different ages growing on contiguous parts of what appear to be identical habitats.

Relative productivity	Habitat type	Age in yrs.	Height in ft.	Site index	Difference based on old stand
Low	*Pinus/*	104	81	80	
	Agropyron	56	40	62	—18
	Pinus/	134	75	65	
	Agropyron	56	42	64	— 1
	Pinus/	149	97	78	
	Purshia	37	32	69	— 9
	Pinus/	208	102	73	
	Purshia	61	47	66	— 7
Fair	*Pseudotsuga/*	117	104	95	
	Calamagrostis	50	46	74	—21
	Pseudotsuga/	64	68	90	
	Calamagrostis	37	35	74	—16
	Pseudotsuga/	79	80	92	
	Calamagrostis	44	43	77	—15
	Pseudotsuga/	93	79	83	
	Calamagrostis	41	34	68	—15
Good	*Pinus/*	91	96	102	
	Symphoricarpos	56	51	74	—28
	Pinus/	97	91	93	
	Physocarpus	39	36	72	—21
	Pinus/	72	83	101	
	Physocarpus	46	45	77	—24

rate of the tree on each of the soil categories studied! Perhaps this simple but important procedural error accounts for some if not all alleged failures of the vegetative indicator concept in the U.S.A. despite its general acceptance in northwestern Europe and southeastern Canada. As pointed out above (Table 1), vegetative indicators do indeed appear to have low value in eastern Washington and northern Idaho if the raw data are converted into site index curves.

The Possibility of Refinement

The vegetative indicator method, as applied to *Pinus ponderosa* in eastern Washington and northern Idaho, allows extremely rapid mapping of the land surface according to the expected growth rates of natural stands of pine, and according to the hazard of disease caused by *Arceuthobium campylopodum*.

Although prediction of site quality as yet plays a small role in forestry in the northern Rocky Mountains, economics is forcing serious consideration of probable growth rates before each site is planted. Some think a highly refined and therefore accurate system of site evaluation is not only desirable but possible, not only as a guide to planting but for interpretation and extrapolation of experimental work. In this view the four growth-rate categories suggested by the vegetative indicator method are rather crude. Although clearly different from each other, there is much variation with the categories. It is entirely possible

that more refined synecology might provide a more finely divided scale of indicator groupings, but there is good reason to doubt that vegetation, soil, or any other criterion will permit a very accurate prediction of growth rates.

The data in Table 2 suggest that unpredictable events in the history of a stand have marked influence on the average rate of height growth on good and poor sites alike. Such factors probably include (1) intensity of a forest fire as it alters fertility from former levels on the same site, (2) timing of the fire, consequently the start of the new stand, in relation to major climatic fluctuations, (3) injury due to insects or fungi, grazing damage, wind-breakage, frost, winter drouth, etc., which the trees may experience then later conceal under new layers of wood. A given stand may happen not to have had its genetically determined maximum growth rate impaired by any of these factors, but at the opposite extreme all the factors may have had cumulative influence in dwarfing the trees. These are the variables that must enter into the fire-line differences shown in Table 2. The magnitude of these differences in growth rates of paired stands provides a critical test for *any* proposed method of predicting growth rates. They suggest that the growth of the tree on a site provides a highly imperfect base for appraising habitat potentialities directly or for calibrating either vegetation or soils for this purpose. Hence, the development of a highly refined scale of site evaluation seems impossible of attainment. The most likely approach would be to base the curve representing full potentialities of the habitat type only on the growth rates of the best stands found in each age group.

Within any one habitat type one could scarcely question the theoretical existence of infinite small steps along multidirectional gradients in soil and climate which could affect average growth rate, and this must be added to the influence of other components of environment that operate in an erratic fashion (e.g. weather extremes, biotic factors). It is therefore remarkable that any consistent differences among habi-

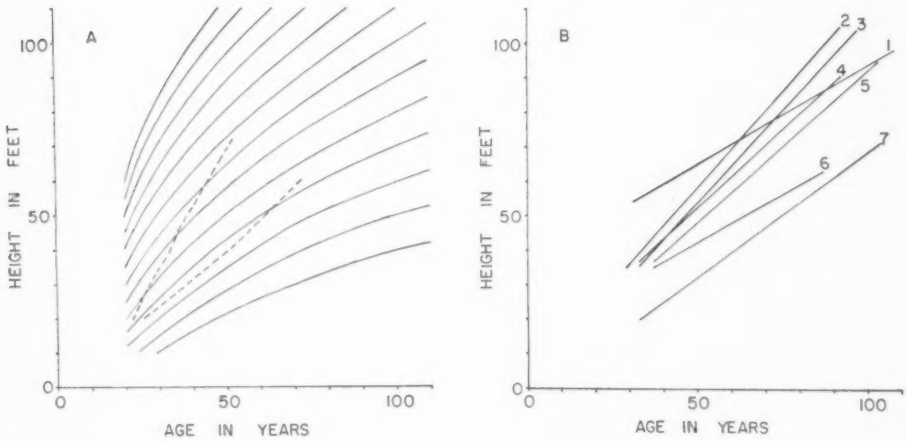


FIGURE 2. A. *Site index curves for* Pinus ponderosa *according to data provided by Meyer (1938), in relation to actual growth of five trees in each of two stands as determined by analyses of felled trees. Upper dashed line represents a* Pinus/Physocarpus *stand, lower dashed line a* Pinus/Symphoricarpos *stand.* B. *Most probable height-age trends according to regression analyses. Numbering corresponds with habitat types listed in Table 3.*

tats can be demonstrated. Conformity of the vegetational and tree-growth categories lends support to the validity and practicality of the vegetation classification.

In Finland the vegetative indicator concept has been studied for half a century and has become the standard means of forest land evaluation. When this system was tested in Sweden it was found that the indicator significance of a given forest undergrowth type differed significantly according to altitude. It is possible that some of the variation in height growth shown in each of the scattergrams in Figure 1 may be accounted for by differences in elevation, for within one habitat type there was often more than 2,000 feet difference among some of the stands studied. Also some of the *Pinus/Symphoricarpos* and *Pinus/Physocarpus* stands used were in the narrow strips of timber that extend from the forested mountains outward into the grassland of the adjacent basal plain. However, the dots on the scattergrams representing these stands located below average timberline do not fall near the lower margin of the pattern, showing that there is a useful degree of homogeneity within a habitat type regardless of wide differences in macroclimate.

Lynch (1958), working in an area that includes northern Idaho and eastern Washington, has also been concerned about "differences in site index estimates as great as 20 units that are often obtained from . . . adjacent stands which, judging on the basis of soil, slope, aspect, and surface vegetation are growing on identical sites." He studied 24 paired stands, the members of each pair differing in density but not age, presumably a result of partial thinning by fire. After detailed biometric analyses, he concluded that the differences in rates of height growth are a result of intraspecific competition associated with different population densities. His conclusions are unusual in forestry literature in that he finds *low* population density of no significance for height growth (see Spurr 1952, Bruce and Schumacher 1942), whereas extreme crowding alone is claimed to reduce rate of height growth.

Since the writer avoided both open and very dense stands, his criticisms of Meyer's data as they apply to this region would seem to be uncomplicated by the density factor. The records kept show that densest stands are not represented among the lowest dots on the scattergrams, as would be the case if they had been dense enough to have had height growth impaired. Thus, variable tree density would not seem to be a measurable component of the height-age variation found within each habitat type.

There are two significant points of agreement between Lynch's conclusions and those of the present study. His curves for stands of average density, as well as my curves based on habitat types, show considerably more diversity in shape than is found in Meyer's site index curves. Secondly, when the stem analysis data in Figure 2A of this paper are superimposed on the curves representing Lynch's data (his Fig. 7D) there is very close agreement, both sources of data differing from Meyer's curves in recognizing more rapid rates of growth between the ages of 25 to 70 years, at least.

Biometric Analyses

As a check on the interpretation of the scattergrams regression analyses were kindly furnished by T. S. Russell of the Computing Center, Washington State University.

Regression lines were constructed of all measurements where the average age of the stand was less than 110 years, it being judged from the pattern of the scattergrams that the age range of 29 to 109 years would represent largely the relatively straight part of a theoretically sigmoid growth curve. Regression analyses (Fig. 2B, Table 3) confirmed the order of rating based on visual inspection of the scattergrams, and suggest that definitely less than seven useful site qualities are indicated by the vegetation of seven habitat types. However, precise interpretation of such bio-

TABLE 3. Summary of biometric analysis of data for stands less than 110 years of age.

Habitat types	No. of Stands	Regr. Equation (Y=ft.; X=yrs.)	95 percent Confidence Interval (ft./yr.)
1. *Abies/Pachistima*	19	Y= 35.99 + 0.58 X	0.28 — 0.88
2. *Pseudotsuga/Physocarpus*	20	Y= 3.31 + 1.11 X	0.72 — 1.50
3. *Pinus/Physocarpus*	21	Y= 1.02 + 1.07 X	0.70 — 1.44
4. *Pinus/Symphoricarpos*	32	Y= 6.59 + 0.91 X	0.61 — 1.21
5. *Pseudotsuga/Calamagrostis*	18	Y= 3.70 + 0.89 X	0.72 — 1.06
6. *Pinus/Purshia*	9	Y= 1.33 + 0.70 X	0.35 — 1.05
7. *Pinus/Agropyron*	17	Y= −5.10 + 0.85 X	0.55 — 1.15

metric data is not justified when the actual age of the trees is never known, and especially when, for the sake of objectivity, a value of 10 years for growth to breast-height is used for all habitat types. Actual growth rates of trees, when stratified according to habitat types, do not form a series of harmonic lines such as postulated by site index curves. Instead the lines for *Abies/Pachistima* and *Pinus/Purshia* cut freely across the others, and all cross the site index curves.

When the regression lines are extrapolated backwards toward zero age, most of them approximate zero height at zero age. Small deviations from the theoretical zero height-zero age point are not important, as the growth rates are not uniform starting from germination. The outstanding feature of these extrapolations is the high deviation of +36 years at zero age for pine growing on the *Abies/Pachistima* h.t. This regression line as well as the raw data in Fig. 1 indicate that for perhaps 50 years of its life on this habitat the tree grows exceptionally well, but soon thereafter the rate declines sharply. It appears to be this juvenile vigor, which is constantly thereafter included in the average age of the plant, that alone keeps the height-age value above that of other habitats except late in the life of the tree. For a 50-year timber rotation the *Abies/Pachistima* habitat is clearly the most productive, but for a 100-year rotation three other habitats are superior (Fig. 2B).

On the *Thuja-Tsuga/Pachistima* habitat type, which is still cooler and wetter than the *Abies/Pachistima* habitat type, the growth rate of planted *P. ponderosa* (almost none grows there naturally) declines so strongly in a few years (Daubenmire 1952) that plantations are complete failures on such sites. There is thus good evidence that, in the region under study, the growth of *P. ponderosa* begins to suffer on sites farther up the moisture-temperature gradient than the *Pseudotsuga/Physocarpus* habitat type, with decline starting earlier and being more marked the farther up the sequence.

Key to Habitat Types Studied

Most forest stands encountered in the field have been burned or grazed, and so support an admixture of species indicative of disturbance. Yet the valuable indicators remain for those who know what to look for. The oft-expressed notion held by many American foresters that lower vegetation is of no value on disturbed lands is not founded on detailed study, but upon impressions resulting from the great differences in physiognomy that are induced by disturbance, but which are really superficial and can be treated accordingly after the synecology of a forest mosaic has been worked out. A short key can be constructed to the seven habitat types considered in this study making use of only a

few of the most distinctive botanical characters of each habitat, which usually are apparent despite any disturbance. For further description of the habitats see Daubenmire 1952.

The habitat types have been named after the species dominant under climax conditions, so that the names do not necessarily reflect present dominants of each site. Thus south of the limits of Pleistocene glaciation a stand of *Pinus ponderosa* with an understory of *Ceanothus sanguineus* plus a liberal sprinkling of young *Pseudotsuga* would certainly occur within the environment range, and exhibit the growth characteristics of a *Pseudotsuga/Physocarpus* habitat type. Therefore names are no more absolutely diagnostic in synecology than in taxonomy, where a *Liriondendron* tree may be called *tulipifera* for years before it produces a flower, and *Abies arizonica* can occur in Colorado.

Pinus ponderosa the sole arborescent conifer (rare stragglers of other taxa are to be ignored if their reproductive success seems inadequate to maintain a substantial population)

Undergrowth dominated by xerophytic grasses (*Agropyron spicatum, Festuca idahoensis, Koeleria cristata, Stipa* spp., *Bromus tectorum*) and practically never including relatively mesophytic grasses such as *Poa pratensis, Calamagrostis rubescens* or *Elymus glaucus*; shrubs very sparse if present at all:

PINUS PONDEROSA/AGROPYRON SPICATUM h.t.

Undergrowth with conspicuous amounts of shrubs

Purshia tridentata well represented; grasses as in the *Pinus/Agropyron* h.t.:

PINUS PONDEROSA/PURSHIA TRIDENTATA h.t.

Purshia tridentata absent

Shrubs consisting of only the *Symphoricarpos albus* union (i.e., one or more of: *Symphoricarpos albus, Rosa ultramontana, R. spaldingii, Spiraea betulifolia, Berberis repens, B. aquifolium*); *Poa pratensis* and *Elymus glaucus* common:

PINUS PONDEROSA/SYMPHORICARPOS ALBUS h.t.

Undergrowth similar to the above, but with the addition of a good representation of the *Physocarpus* union (i.e., one or more of *Physocarpus malvaceus, Holodiscus discolor, Ceanothus sanguineus*):

PINUS PONDEROSA/PHYSOCARPUS MALVACEUS h.t.

Pseudotsuga and/or *Abies grandis* present (*Thuja, Tsuga, Picea,* and *Abies lasiocarpa* occurring as stragglers if at all)

Pseudotsuga menziesii the tree most successful in reproduction; few if any species of the *Pachistima* union[1] present

Calamagrostis rubescens well represented; shrubs, if any, as in *Pinus/Physocarpus* h.t.; within glaciated region:

PSEUDOTSUGA MENZIESII/CALAMAGROSTIS RUBESCENS h.t.

Calamagrostis rubescens seldom well represented; shrubs as in *Pinus/Physocarpus* h.t.; within or beyond the glaciated region:

PSEUDOTSUGA MENZIESII/PHYSOCARPUS MALVACEUS h.t.

Abies grandis the tree most successful in reproduction; the *Pachistima* union represented by a number of taxa:

ABIES GRANDIS/PACHISTIMA MYRSINITES h.t.

[1]Representative members: *Actaea arguta, Adenocaulon bicolor, Anemone piperi, Asarum caudatum, Bromus vulgaris, Clintonia uniflora, Coptis occidentalis, Cornus canadensis, Galium triflorum, Lastrea dryopteris, Linnaea borealis, Lonicera utahensis, Osmorhiza spp., Pachistima myrsinites, Rosa gymnocarpa, Smilacina stellata, Taxus brevifolia, Tiarella unifoliata, Trillium ovatum, Viola rotundifolia.*

Summary

The rate of height growth of *Pinus ponderosa* has been studied in 153 stands in eastern Washington and northern Idaho. When the data are grouped according to habitats, these based on the plant associations that are climax for the sites, good correlations are obtained, so that vegetation, whether climax or not, serves as a rapid and useful means of predicting in advance the probable growth rate of the pine. Susceptibility of the tree to infection by *Arceuthobium* is also correlated with these vegetative indicators. The data suggest that the site index curves that have been used for *Pinus ponderosa* over a wide area are not valid in the region under study. A key is provided for the identification of the seven habitat types supporting natural stands of *Pinus ponderosa* in the region studied.

Literature Cited

BRADSHAW, A. D. and R. W. SNAYDON. 1959. Population differentiation within plant species in response to soil factors. Nature 183:129-130.

BRUCE, D. and F. X. SCHUMACHER. 1942. Forest mensuration. pp. 425. McGraw-Hill Book Co., New York.

CARMEAN, W. H. 1956. Suggested modifications of the standard Douglas-fir site curves for certain soils in Southwestern Washington. For. Sci. 2:242-250.

DAUBENMIRE, R. 1943. Soil temperature versus drought as a factor determining lower altitudinal limits of trees in the Rocky Mountains. Bot. Gaz. 105:1-13.

———. 1946. Radial growth of trees at different altitudes. Bot. Gaz. 107:462-467.

———. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Mono. 22: 301-330.

———. 1960. An experimental study of variation in the *Agropyron spicatum-A. inerme* complex (ms.)

HABECK, J. R. 1958. White cedar ecotypes in Wisconsin. Ecol. 39:457-463.

LORENZ, R. W. and J. N. SPAETH. 1947. The growth of conifers on prairie soil. J. For. 45:253-256.

LYNCH, D. W. 1958. Effects of stocking on site measurement and yield of second-growth ponderosa pine in the Inland Empire. U. S. For. Serv., Intermtn. For. and Range Exp. Sta., Res. Paper 56. pp. 36.

MCMILLAN, C. 1956. The edaphic restriction of *Cupressus* and *Pinus* in the coastal ranges of central California. Ecolo. Mono. 26:177-212.

MEYER, W. H. 1938. Yield of even-aged stands of ponderosa pine. U. S. Dept. Agric. Tech. Bul. 630. pp. 54.

SHEPHERD, R. F. 1959. Phytosociological and environmental characteristics of outbreak and non-outbreak areas of the two-years cycle spruce budworm, *Choristoneura fumiferana*. Ecol. 40:608-620.

SPURR, S. H. 1952. Forest inventory. pp. 476. Ronald Press Co., New York.

———. 1956. Soils in relation to site-index curves. Soc. Amer. For. Proc. 1955:80-85.

TISDALE, E. W. and A. MCLEAN. 1957. The Douglas fir zone of southern British Columbia. Ecol. Mono. 27:247-266.

Crown Competition—A Measure of Density

BY
JOHN E. KRAJICEK
KENNETH A. BRINKMAN
SAMUEL F. GINGRICH

THE MEASUREMENT of stand density has been one of the most trying problems in forestry. Many measures have been proposed but a completely satisfactory one has not yet been found.[1] In an effort to help solve the problem, a new measure of stand density, developed at the Central States Forest Experiment Station, is presented here.

Density, as foresters commonly use the term, is the relation between the number of trees or some volumetric or areal unit to a specific area, usually 1 acre. In effect, then, a density measure is intended to help determine the relation of the average tree in the stand to the maximum growing space it could utilize on the one hand, and the minimum growing space necessary to live on the other. It is within this range that the forester wishes to maintain density to fully utilize the site for maximum production of desired usable volume.

The maximum growing space that can be used by a tree of small diameter is, of course, less than that for a tree of larger diameter. The problem of determining the growing-space/tree-size relations is complicated by the effects of present and past density on both stem diameter and crown size. So for a given species of specified d.b.h., the size of the crown may vary greatly. (Although trees compete for moisture and nutrients as well as for light, it would be impractical to measure and relate size of root systems to degree of competition between trees. In fact, it is probable that crown area may be an indicator of root area and thus a measure of such subterranean competition.[2]) The only place where the crown/d.b.h. relations are not confounded by competition from other trees is in the *open-grown* tree. So the new method described here is based on the relation of crown area to d.b.h. of open-grown trees.[3]

---

[1]The authors recognize the vast amount of literature on the subject of stocking and density, but believe a review of this work would add very little to the presentation of the new measure given in this report. Good discussions of stocking and density measures are given by:

Spurr, Stephen H. Forest inventory. The Ronald Press Co. New York. 476 pp. 1952 and

Bickford, C. Allen, et al. Stocking, normality, and measurements of stand density (Report of S.A.F. committee on stocking). J. For. 55:99-104. 1957.

[2]Büsgen, M. and Münch, E. The structure and life of forest trees, page 273. New York, 1931.

[3]A brief presentation of this subject is given in Station Note 108 "Crown development: an index of stand density" by Krajicek and Brinkman. Central States Forest Experiment Station, U. S. Department of Agriculture, 1957.

The authors are respectively Research Forester, Silviculturist, and Research Forester, Central States Forest Experiment Station, Forest Service, U. S. Department of Agriculture. Manuscript received Nov. 24, 1958.

Development of Crown-Width/D.B.H. Relations

To establish the relation between width of crown and d.b.h. for open-grown trees, 340 open-grown trees were measured in eastern Iowa: 88 white oaks (*Quercus alba* L.), 60 black and red oaks (*Q. velutina* Lam. and *Q. rubra* L.),[4] 35 hickories (*Carya ovata* (Mill.) K. Koch), and 157 Norway spruce (*Picea abies* (L.) Karst.). As nearly as could be determined, each tree had developed without competition throughout its entire life. To maintain uniformity in selecting sample trees, only those that met the following specifications were included in the sample:

1. Crown free of competition on all sides.
2. Limbs extending to the ground on small trees and nearly so on larger trees.
3. Lowest branches the longest, or at least as long as those above. (This eliminated trees that had been released from competition in the past and on which the lower portion of the present crown originated from epicormic branches.)
4. For small trees (less than 16 feet tall), no forking in the entire length; for larger trees, no forking of the bole below 16 feet. (This limited the sample to trees that were of the type that would be favored in the forest stand, except for limbiness and excessive taper.)
5. No evidence of pruning, shearing, browsing, decadence, storm damage, or serious insect damage.
6. Tree apparently not of sprout origin.

The smaller hardwood sample trees were found in old fields, on road rights-of-way, and on recently cutover, ungrazed areas where the sample trees originated after cutting. The larger hardwood sample trees were found in timbered pastures, cemeteries, and, to a limited extent, in residential areas. Norway spruce sample trees were found principally in cemeteries and parks located in or near small towns, in recently established windbreaks, and occasionally in residential areas.

Crown width of each sample tree was measured twice, the second measurement at right angles to the first, and the results averaged. Regression analyses of the data showed definitely that the crown width of an open-grown tree is closely related to its d.b.h.

Site quality was not determined directly for the locations where the sample trees were found. For the species examined, open-grown trees were somewhat shorter than their forest-grown counterparts of the same diameter on similar soils and aspects. Most of the hardwood sample trees were found on forest soils where site indices ranged from 45 to 75. The rest were found on prairie or transitional soils in which the productivity of the similar forest soils was known to range from poor to good.

Differences in the relation between crown and stem diameter among the hardwood species sampled were small (Fig. 1). The differences between the red oaks and white oak and between white oak and hickory were not statistically significant at the 5-percent level. The difference between hickory and red oaks was significant, but just barely so. For simplicity in application all hardwood data were combined (Fig. 2).

Crown width and d.b.h. for Norway

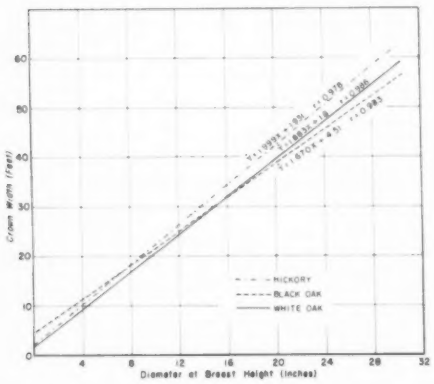


FIGURE 1. *Relation of crown width to d.b.h. for open-grown hickory, white oak, and black oaks.*

[4]Hereafter "red oaks" refers to both *Q. velutina* and *Q. rubra*.

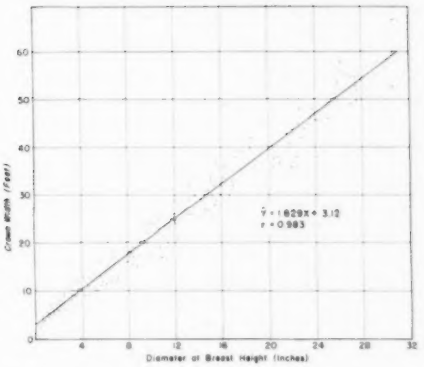


FIGURE 2. *Open-grown crown width–d.b.h. relation for combined hickory, white oak, and black oaks.*

spruce also were highly correlated (Fig. 3.). The differences between the hardwoods and Norway spruce were highly significant at the 1-percent level.

Since such a close relationship exists between the crown diameter and d.b.h. of open-grown trees, and this relationship is nearly constant within a species, it may be inferred that the crown of a tree of given d.b.h. cannot occupy more than a certain area even with unlimited growing space.

Development of an Index of Crown Competition

Knowing the average crown width and assuming that crowns of open-grown trees tend to be circular, the approximate area covered by the crown can be readily computed. The percentage of an acre occupied by a vertical projection of the crown is obtained by dividing the area in square feet by 435.6. For example, an open-grown Norway spruce with d.b.h. of 16 inches has a crown width of approximately 26 feet (Fig. 3), or crown area of 531 square feet (1.22 percent of an acre). This value has been termed "maximum crown area" (MCA), because it expresses, *in terms of percent of an acre*, the maximum area that could be occupied by the crown of a tree of specified d.b.h.

To determine MCA values for each tree in a stand would be time consuming. However, from the least squares solution of crown width and d.b.h., a formula can be derived that simplifies the procedure:

The MCA value of a tree with a crown diameter of CW is

$$MCA = \frac{\pi\,(CW)^2}{\frac{4}{435.6}}$$

$$= 0.0018\,(CW)^2$$

From the regression analysis of the combined oak-hickory data (Fig. 2),

$$CW = (1.829D + 3.12)$$

where D = d.b.h.

and

$$(CW)^2 = 3.345D^2 + 11.413D + 9.734$$

Therefore,

$$MCA = 0.0060D^2 + 0.0205D + 0.0175$$

Similarly, the formula of MCA values for Norway spruce is

$$MCA = 0.0031D^2 + 0.0239D + 0.0460$$

With the MCA values determined, it is not difficult to compute the *minimum* number of open-grown trees per acre that are theoretically required to produce a complete canopy (assuming that crowns are distorted sufficiently to fill all voids in the canopy, but without reducing the crown area of the individual trees). If a tree has a d.b.h. of 16 inches and an MCA of 1.22 (as in the previous example), then 82 open-

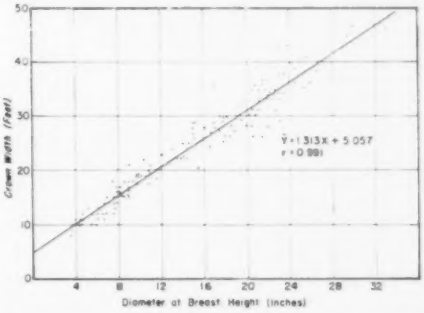


FIGURE 3. *Relation of crown width to d.b.h. for open-grown Norway spruce.*

TABLE 1. Determination of the CCF for an even-aged upland oak stand, site index 60, age 50 (Schnur 1937).

D (d.b.h.)	N (Number of trees per acre)	DN	D^2N	Check using MCA values	
				MCA per tree	Total MCA
				Percent	*Percent*
1	10	10	10	0.044	0.440
2	29	58	116	.082	2.378
3	50	150	450	.133	6.650
4	63	252	1,008	.196	12.348
5	77	385	1,925	.270	20.790
6	78	468	2,808	.356	27.768
7	66	462	3,234	.455	30.030
8	49	392	3,136	.566	27.734
9	31	279	2,511	.688	21.328
10	17	170	1,700	.822	13.974
11	7	77	847	.969	6.783
12	3	36	432	1.128	3.384
13	1	13	169	1.298	1.298
Total	481	2,752	18,346		174.905 (CCF)

$CCF = 0.0060(18,346) + 0.0205(2752) + 0.0175(481) = 174.91$

grown trees of that size could cover an acre completely ($82 \times 1.22 = 100$ percent, or sum of MCA values equals 100). Using MCA values for other d.b.h. classes, any combination of open-grown trees of various diameters whose MCA values total 100 for an acre theoretically could have a closed canopy.

To avoid confusion in using one term—MCA—to express the area requirement of both a single tree and a sum of trees, another expression, "Crown Competition Factor" (CCF), has been coined to represent the sums of the MCA values for an acre. Crown Competition Factor is defined as the sum of MCA values for all trees in the stand, divided by the area in acres. It is used as an expression of stand density. These summations can be expressed by using the previous formulas in the following form:

For oak-hickory stands,

$$CCF = \frac{1}{A}\left[0.0060\left(\Sigma D_i^2 N_i\right) + 0.0205\left(\Sigma D_i N_i\right) + 0.0175\left(\Sigma N_i\right)\right]$$

and for Norway spruce,

$$CCF = \frac{1}{A}\left[0.0031\left(\Sigma D_i^2 N_i\right) + 0.0239\left(\Sigma D_i N_i\right) + 0.0460\left(\Sigma N_i\right)\right]$$

where

D_i = individual d.b.h. or d.b.h. class
N_i = number of trees in d.b.h. class
A = area in acres

An example of the application of the CCF to a specific stand is given in Table 1. All the trees in the stand are used to determine the CCF. In the stand of trees shown in Table 1, nearly 60 percent of the Crown Competition Factor is contained in trees less than 8 inches d.b.h. To consider

only those trees larger than a specified lower diameter limit will result in a low CCF and will not represent the actual competition in the stand. It is known, of course, that the larger trees have an adverse effect on the growth rate of the smaller. It is more difficult to assign an effect of the small trees on the growth of larger ones. Where moisture is a limiting factor at any time during the growing season, the smaller trees probably have an adverse effect on the growth of the larger trees.

One other precaution is necessary. When computing the CCF from stand tables, the actual number of trees in each diameter class should be used rather than the diameter of the tree of average basal area and total number of trees. If the latter procedure is followed, excessive errors may result when the diameter distribution deviates greatly from the normal curve.

Results and Discussion

It is obvious that maintaining stand density below CCF 100 from time of establishment to maturity would normally produce low-quality trees, especially if they were not pruned artificially. Greater density (with a higher CCF value) would be accompanied by a reduction of the actual or effective live crown of the average tree in the stand.

Density will not increase indefinitely, of course. A number of even-aged pure oak stands in Iowa consistently showed a ceiling density of about CCF 200, when all trees in the stand were included. Similarly, the average CCF for 52 even-aged oak plots, each 0.2 acre in size, located throughout southeastern Ohio and selected for full stocking was exactly 200.[5] A consistent ceiling probably exists for all other species also, but it is probably different from that found for oaks.

[5]These unpublished data on which the computations are based were collected and furnished by Willard Carmean and Stephen G. Boyce, Soil Scientist and Research Forester, respectively, Central States Forest Experiment Station.

At least three things account for differences among species in the maximum CCF they can obtain. One is their crown area development when there is no competition. Another is the basic shape of the crown, such as conical, parabolic, etc. Also, tolerance may be a factor. For example, measurements over an 8-year period in heavily stocked oak-hickory plots show a slightly higher CCF than those found in pure oak stands, probably because of the greater tolerance of hickory. Some of the Ohio plots cited above also had CCF values in excess of 200, but these too contained some of the more tolerant species.

To further confirm the consistency of the values found in field tests, the formula for oak-hickory was applied to stand tables for even-aged upland oaks. Except for high values in younger stands on the poorer sites, the CCF values show great uniformity (Table 2).

No Norway spruce stands were available for field testing of the formula. The similarity of crown widths among the oak species suggested that perhaps a given crown width/d.b.h. relation may be rather common within a genus. With this thought, the Norway spruce formula was applied to stand table data for Sitka spruce and west-

TABLE 2. Application of CCF to stand table data[1] for even-aged upland oaks.

Age	(CCF values by age class and site index) Site index				
(years)	40	50	60	70	80
10	301	249	219	190	166
20	218	210	188	180	181
30	184	183	178	176	167
40	171	170	168	165	160
50	169	169	175	173	173
60	171	171	176	175	169
70	165	168	172	170	165
80	168	176	173	172	164
90	175	179	177	174	164
100	178	182	177	175	166

[1]Schnur, G. Luther. Yield, stand, and volume tables for even-aged upland oak forests. U. S. Dept. Agric. Tech. Bull. No. 560, Table 37, 1937.

ern hemlock (Table 3). These data are primarily for stands in Washington and Oregon, yet the CCF values for the age-site classes enclosed by the broken line are quite consistent, except for age 140, site index 160. The latter may be an error in the original table.

A comparison of oak-hickory and Norway spruce stands of the same density as measured by crown competition reveals a striking difference in their structure. For example, a Norway spruce stand composed of 16-inch trees would have more than half again the number of trees and basal area per acre as an oak-hickory stand with trees of like size and the same CCF.

Comparison With Other Measures

A thorough comparison of CCF with other measures of stand density would require much space. A brief comparison serves to illustrate the relation between CCF, basal area per acre, and Reineke's stand-density index (Table 4). It is of interest to note that when CCF is held constant over a range of average stand diameters, basal area per acre changes at a rate that is typical of most even-aged stands. CCF does not show a consistent relationship with stand-density index. Although a CCF of 100 (which might indicate minimum density for full site utilization) is approximately associated with a stand-density index of 110 percent for stands with average diameters as shown, the relationship of number of trees to average stand diameter is curvilinear on log-log paper for any given CCF value, whereas stand-density index is linear. However, this does not represent a deterrent to the application of CCF. Approximate full stocking in terms of stand-density index (240) results in CCF values from 197 to 262 as shown in column 6 of Table 4. Again, one could conclude *in general* that a CCF of 200 (which might represent maximum density for full site utilization) is approximately equivalent to a stand density index of 240 for stands with an average diameter of from 5 to 15 inches.

In comparing "D plus" and "D times" spacing[6] with CCF spacing, it is apparent

[6]Rules of thumb used as thinning guides: Using the "D plus" rule, spacing of trees in feet is equal to the diameter of the trees in inches plus a constant; using the "D times" rule, spacing in feet is equal to tree diameter in inches times a constant.

TABLE 3. Application of CCF to stand table data[1] for even-aged Sitka spruce and western hemlock. (CCF values by age class and site index.)

Age	Site index							
(years)	60	80	100	120	140	160	180	200
40	1184	635	412	345	320	292	275	269
60	427	351	332	299	288	276	270	267
80	356	327	306	293	284	283	280	276
100	326	299	296	288	284	285	285	285
120	304	296	291	286	285	285	287	289
140	291	289	286	286	286	241	290	287
160	286	285	287	287	287	291	296	-----
180	283	282	281	283	288	288	292	-----
200	279	280	280	284	289	293	294	-----

[1]Meyer, W. H. Yield of even-aged stands of Sitka spruce and western hemlocks. U. S. Dept. Agric. Tech. Bull. No. 544, Table 36, 1937.

Dash lines indicate limits of basic data.

TABLE 4. Comparisons of CCF with basal area and stand-density index[1] for theoretical oak-hickory stands of various average diameters.

Average d.b.h.[2] (inches)	When CCF is 100:			When stand-density index is 240:		Basal area per acre when:	
	Trees per acre	Basal area per acre	Stand-density index	Trees per acre	Equivalent CCF	CCF = 200	SDI = 240
	Number	*Square feet*	*Percent*	*Number*	*Percent*	*Square feet*	*Square feet*
2	1,220	26.8	92	3,177	262	53.7	69
5	370	50.3	122	730	197	101	100
10	122	66.5	122	240	197	132	131
15	60	73.6	115	125	209	146	153
20	35.3	77.0	107	78.9	223	154	172
25	23.4	79.8	102	55.1	236	159	188

[1]Reineke, L. H. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46: 627-638. 1933.
[2]Calculated from average basal area per tree. (Used in the example to facilitate comparisons with stand-density index. As stated in the text, the actual number of trees in each diameter class should be used to compute CCF.)

TABLE 5. Spacing of trees for a CCF of 100 and equivalent "D plus" and "D times" constants for theoretical stands of oak-hickory and Norway spruce of various average diameters.

Average d.b.h.[1] (inches)	Oak-hickory			Norway spruce		
	CCF spacing	"D plus" constant	"D times" constant	CCF spacing	"D plus" constant	"D times" constant
	Feet	*Feet*	*Unit*	*Feet*	*Feet*	*Unit*
2	6.0	4.0	3.00	6.8	4.8	3.40
5	10.8	5.8	2.16	10.3	5.3	2.06
10	18.9	8.9	1.89	16.1	6.1	1.61
15	26.9	11.9	1.79	21.9	6.9	1.46
20	35.1	15.1	1.76	27.7	7.7	1.38
25	43.1	18.1	1.72	33.6	8.6	1.34

[1]Calculated from average basal area per tree.

that spacing based on CCF will not result in a constant factor for stands of different average diameters (Table 5). An examination of these "constants" substantiates the findings of Stahelin[7] and others that diameter plus a constant results in too much basal area with large trees and too little with small trees.

[7]Stahelin, R. Thinning even-aged loblolly and slash pine stands to specified densities. J. For. 47:538-540, illus. 1949.

It should be emphasized that CCF is not essentially a measure of crown closure. Theoretically, complete crown closure can occur from CCF 100 to the maximum for the species (in oaks, approximately CCF 200). Instead of estimating crown closure, CCF estimates the area available to the average tree in the stand in relation to the maximum area it could use, if it were open grown.

Conclusions

There is good evidence to indicate that the CCF method of measuring density can be applied to even-aged stands of hardwoods and conifers. Moreover, although field tests of the method have been confined to even-aged stands, in theory it can be used for uneven-aged stands equally well. The method adjusts accurately to variations in diameter distribution and to the potential crown space requirements for the individual trees.

Traditionally, researchers have insisted that the ideal measure of density should be correlated with growth and yield and independent of stand age. On this premise CCF has shown up well in preliminary tests. In stand density studies in even-aged oak net basal area growth (accretion less mortality) is at a maximum when CCF is 135. This holds true for stands 25, 50, and 90 years old, with corresponding average basal area per acre of 71, 86, and 96 square feet respectively. The growth data cover an 8-year period for the two younger age classes and a 4-year period for the other.

Several important points should be emphasized:

1. Relatively few measurements of *truly* open-grown trees are required to provide a basic CCF equation for a species.

2. The ceiling of about CCF 200 for oak density should not be assumed for other species, even when crown widths are found to be similar. Relative tolerance and shape of crown (conical, parabolic, etc.) determine the maximum densities attainable by a species.

3. In stands having mixtures of species with different crown characteristics and tolerance, the determination of CCF may need to be handled by proportional representation.

The CCF is as simple to apply as basal-area tables, but, unlike basal-area control, interpretation of values does not depend upon diameter distribution of a specific type or range. The Crown Competition Factor, based on a verified relationship between crown width and d.b.h., should measure competition more acurately than the methods presently used.

Summary

Measurements of several hundred oak, hickory, and Norway spruce disclosed a high degree of correlation between crown width and d.b.h. for open-grown trees of the same species. Apparently this relation is independent of age and site quality. From the open-grown-tree data, formulae were derived which express the maximum percentage of an acre the crown of an open-grown tree of a given diameter and species could occupy.

Theoretically, competition for crown space between trees in a stand begins when all crown space is occupied and each tree crown is equal in area to that of an open-grown tree of the same d.b.h. This condition is taken as a base of 100 for expressing competition among crowns for growing space. From this base, stand density may be expressed as a percentage. For convenience, this percentage is termed the Crown Competition Factor (CCF), because it is an estimate of the competition among crowns for growing space. Preliminary trials indicate that the method is applicable to even-aged stands, and theoretically can be used to advantage in uneven-aged stands. These trials show strong evidence that site and stand age do not influence CCF.

The Influence of Gibberellic Acid on Growth and Fiber Length of Quaking Aspen

BY
DEAN W. EINSPAHR
J. P. van BUIJTENEN

GIBBERELLIC ACID, the metabolic product of the fungus *Gibberella fujikuroi,* is a growth-promoting chemical that has been tried widely on agricultural crops and recently has been the subject of a number of studies having forestry implications.

Some of the earliest tests of this chemical on forest tree species were made by Marth, *et al.* (1956). Their work produced stem growth increases of from 0 to 400 percent, with the conifers showing the least response to the treatments. Since this first work, additional information has been published regarding the influence of gibberellic acid on tree growth by Nelson (1957), Hacskaylo and Murphey (1958), Knight (1958a, b), Schaedle (1958), Swan (1958), and Westing (1959). Most trials have been conducted on young trees with the practical aims of improving early growth and development. Results obtained from these studies range from very promising to disappointing, and are quite variable because of the number of tree species involved and testing methods employed.

Preliminary Trial

The present study was established to investigate the influence of gibberellic acid on growth and fiber properties of quaking aspen (*Populus tremuloides* Michx.). The study was divided into two phases. The first was a greenhouse trial of limited scope designed to give preliminary information regarding methods of application, treatment levels, response time, and the frequencies of reapplication necessary to maintain rapid growth when gibberellic acid was applied as a foliage spray. The second phase was a field trial using the levels of chemical established in the preliminary work.

Quaking aspen seed from an experimental cross made in the greenhouse was planted in 11 8-inch standard clay pots. After five weeks each pot was thinned to 12 good seedlings and at eight weeks of age the treatments listed in Table 1 were applied. This phase of the study was not replicated. The chemical[1] used consisted of a combination of gibberellic acids A and X.

The 500 ppm, 100 ppm, and the 1 ppm treatments were applied as an aqueous spray using Tween 20 to improve coverage and uptake. The spray treatments were reapplied at 2, 4, and 6 week intervals. Spray treatments consisted of a 10-ml solution

[1]The gibberellic acid used was supplied by Abbott Laboratories, North Chicago, Illinois. Additional information regarding chemical composition and methods of handling can be obtained by writing to that company.

The authors are Silviculturist and Geneticist, respectively, at The Institute of Paper Chemistry, Appleton, Wisconsin. They are greatly indebted to Abbott Laboratories, North Chicago, Illinois, for financial support of the study and to Marlin T. Leffler and Norman Leffler of that company for technical assistance in handling and applying gibberellic acid. Manuscript received Mar. 14, 1960.

TABLE 1. Summary of height growth response of aspen seedlings treated with gibberellic acid in the preliminary trial.

G.A. treatment	Frequency of reapplication	Height growth response (treatment *vs.* control)
	Weeks	*Percent*
500 ppm	2	216
	4	451
	6	62
100 ppm	2	214
	4	146
	6	98
10 ppm	2	−14
	4	−14
	6	40
1% G.A. in Lanolin	–	110

applied to each pot of 12 seedlings as a fine mist, using a small electric paint sprayer. The 1 percent gibberellic acid in lanolin paste was applied by encircling the seedling stem with a thin band about ½ inch above the ground line. A toothpick was used for making the application.

The seedlings in this trial were fertilized weekly with a soluble fertilizer and grown in the greenhouse on a 14-hour day. Measurements and observations on treated seedlings were made twice each week and treatments were reapplied as scheduled.

Results of the Preliminary Trial

Table 1 summarizes the height growth response obtained when the treated seedlings were compared with the control seedlings eight weeks after treatment. Figure 1 illustrates the type of growth curves obtained from height measurements and Figure 2 the growth response and the variability of the treated individuals in several of the applied treatments.

Little or no response was obtained with the 1 ppm level at any of the treatment reapplication frequencies. The 1 percent gibberellic acid in lanolin paste gave a response similar to the 100 ppm and the 500 ppm treatment levels. The best treatment in this preliminary trial appeared to be the 500 ppm applied every four weeks.

Reapplication every six weeks resulted in the least response, both at the 100 ppm and the 500 ppm levels. Reapplication every two weeks at 100 ppm and 500 ppm levels resulted in a number of individuals in each pot with long, narrow leaves, light-green leaf color, and spindly, crooked, abnormally formed stems. Response after treatment was rapid and changes in the slope of the growth curves usually were evident within four to six days after applications.

Field Trials of Gibberellic Acid

The second phase of this study involved the application of the results obtained in the preliminary trial to a study aimed particularly at measuring the influence of gibberellic acid on growth and on fiber length of quaking aspen under field conditions. Fiber length was of special interest because

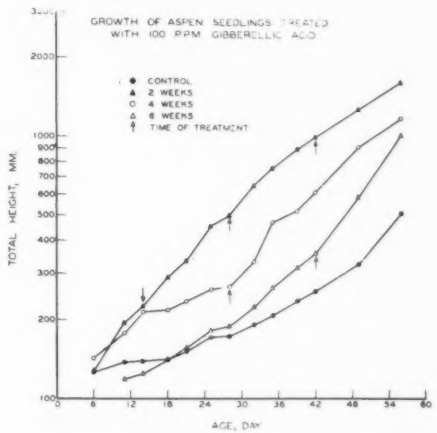


FIGURE 1. *Height growth curves of greenhouse-grown quaking aspen treated with a 100 ppm aqueous gibberellic acid spray. The several curves represent seedlings treated every two weeks, every four weeks, every six weeks, and the control. The arrows indicate the time the treatments were reapplied.*

of its importance in influencing certain strength properties of the paper produced from aspen. Also of interest in this second phase was the further refinement of treatment levels and frequencies of reapplication.

Quaking aspen seed from a controlled experimental greenhouse cross was again used as a source of experimental material. The seed was sown early in March and the seedlings transplanted into plant bands at four weeks of age. At 11 weeks, the treatments listed in Table 2 were applied to a total of 1,760 trees, and the trees then planted in the field. The gibberellic acid treatment levels employed were 250 ppm, 100 ppm, and 10 ppm applied as an aqueous spray and 1 percent gibberellic acid in a lanolin paste. The reapplication frequencies used were every 3, 4, and 5 weeks. The treatments were applied as previously described, the aqueous spray with an electric paint sprayer and the gibberellic acid-lanolin paste as a small band approximately 1 inch above the ground line. Reapplication in the field was made on scheduled days with enough spray used per individual to wet the leaves thoroughly. The gibberellic acid-lanolin paste treatment was not reapplied.

Each treatment was replicated twice, and each replication contained 80 seedlings lined out in a single row spaced within the row at 8 to 10 inches. Weekly height measurements were made on the first 20 individuals in each replication and additional observations (survival, leaf size and color, and dieback) were made periodically during the growing season on all 80 seedlings. Some information regarding the effect of gibberellic acid on root development was obtained by oven drying and weighing the root systems from the first ten individuals from each of the replications.

The time-consuming aspects of fiber measurement work made it desirable to check only certain representative treatments. Two trees of average size from each replication or a total of 4 trees from each selected treatment were sampled by taking a 6- to 8-inch section from the lower portion of the stem. The samples were subsequently chlorited according to the method of Spearin and Isenberg (1947), and stained with congo red. The stained fibers were washed, suspended in the proper concentration and mounted on microscope slides. From each sample 100 fibers (tracheids) were measured on a projector at a magnification of 75×.

FIGURE 2. *Growth response of aspen seedlings treated with gibberellic acid in the preliminary greenhouse trial, 8 weeks after treatment. These aqueous spray treatments were applied every four weeks.*

Results of Field Trial with Gibberellic Acid

Weekly height-growth measurements were made during the growing season and a summary of the measurements is presented in Tables 2 and 3. Several treatments are further illustrated in Figures 3, 4, and 5. Table 2 also provides information regarding survival, percentage of trees showing tip dieback,[2] diameter growth and root development of the treated trees.

Analyses of variance were made on the original data summarized in Table 2. Results of the analyses presented in Table 4 are useful in interpreting treatment effects. The "F" values listed were computed using the error mean square term except in those instances where the level x frequency (L x F) interaction was significant. When the L x F interaction was significant the "F" values for levels and frequencies were computed using the L x F interaction mean square term.

Height growth of the treated individuals in the field trials during the first 8 weeks followed a pattern quite similar, although much less spectacular, than that of the preliminary greenhouse trial. At 8 weeks, as Table 3 illustrates, height growth response of the treated trees when compared with the control trees ranged from 3.4 to 48.9 percent, with the 100 ppm and the 250 ppm treatments showing the greatest response. During the growth period from the 8th to the 14th week, the growth rate of the control trees was quite rapid and at the end of the 16th week, the average height of the control trees was approximately equal or greater than any treatment, except the 100 ppm five-week treatment.

The "F" values for the average height data indicate no significant differences in seedling growth between control and spray treatments, lanolin and spray treatments, and height growth differences resulting from levels or frequencies of reapplication

[2]The dieback of the growing tip appears similar to a disease caused by *Napicladium tremulae* in which young shoots bend over, darken in color, and dry out.

TABLE 2. Growth, survival, and dieback of aspen seedlings treated with gibberellic acid in replicated field trial.

Treatment	Frequency of reapplication (weeks)	Trees planted (No.)	Survival (percent)	Dieback[1] (percent)	Ave. ht. (cm)	Ave. Stem Dia. (mm)	Ave. o.d. wt. roots (g)
Gibberellic acid							
250 ppm	3	158	44.9	14.6	54.5	.33	0.9
	4	155	32.2	15.5	56.8	.28	0.5
	5	157	69.4	11.5	64.1	.43	2.3
100 ppm	3	159	79.2	13.2	60.9	.34	1.0
	4	158	89.2	11.4	52.0	.36	2.1
	5	159	88.7	10.1	78.7	.67	7.4
10 ppm	3	159	91.8	9.4	64.2	.57	7.6
	4	148	98.1	2.5	59.7	.56	6.3
	5	156	96.8	1.9	60.6	.57	7.1
1 percent G.A. in lanolin	–	158	94.9	7.0	49.1	.47	4.7
Control	–	159	92.4	1.9	62.7	.64	8.9

[1]Percent of trees showing growing tip dieback on 7/14/58, after a period of rapid growth.

TABLE 3. Average height and response of aspen seedlings to treatments at the end of 8 and 16 weeks.

Treatment	Frequency of reapplication (weeks)	At 8 weeks		At 16 weeks	
		Ave. ht. (cm)	Response[1] (percent)	Ave. ht. (cm)	Response[1] (percent)
Gibberellic acid					
250 ppm	3	36.8	38.3	54.4	—13.2
	4	39.6	48.9	56.8	— 9.4
	5	33.0	24.1	64.1	+ 2.2
100 ppm	3	36.5	37.2	60.9	— 2.9
	4	33.4	25.6	52.0	—17.1
	5	35.6	33.8	78.7	+25.5
10 ppm	3	32.4	21.8	64.2	+ 2.4
	4	30.0	12.8	59.7	— 4.8
	5	29.0	9.0	60.6	— 3.4
1% G.A. in lanolin	–	27.5	3.4	49.1	—21.7
Control	–	26.6	—	62.7	—

[1]Percent height growth increase or decrease, treated seedlings compared with control seedlings.

of gibberellic acid. A separate analysis using data from the control and 100 ppm 5-week spray treatments only gave a highly significant "F" test. Since in this case the difference includes the effect of the treatment and the influence of soil differences, one should be cautious in interpretation. The differences, however, are of sufficient magnitude to warrant further research using similar concentrations and frequencies of application.

Diameter growth was not checked as

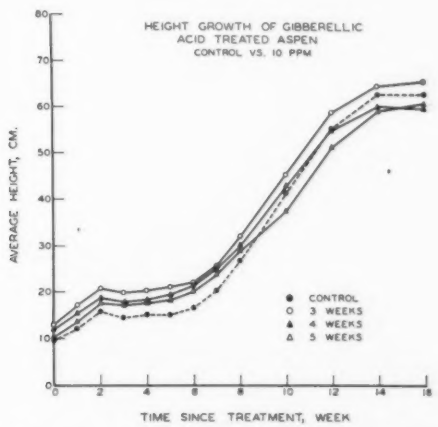


FIGURE 3. *Height growth of quaking aspen treated with 10 ppm gibberellic acid, based on measurements of seedlings in the replicated field trial.*

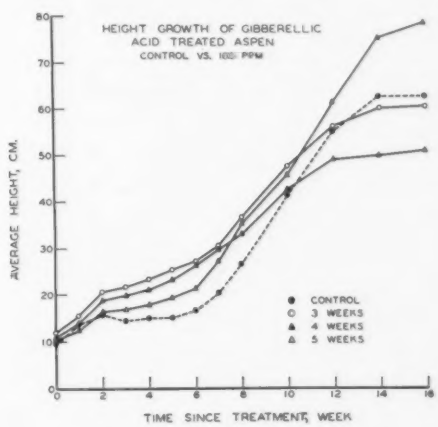


FIGURE 4. *Height growth of quaking aspen treated with 100 ppm gibberellic acid.*

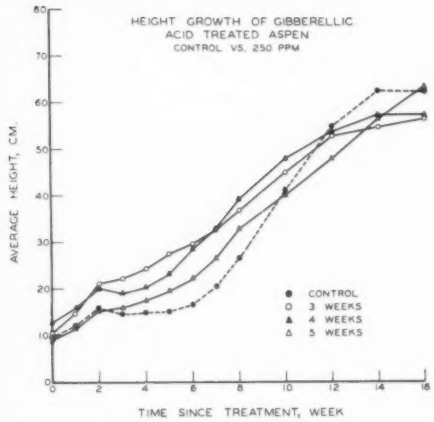


FIGURE 5. *Height growth of quaking aspen treated with 250 ppm gibberellic acid.*

closely as height growth and only stem diameter at the ground line was measured at the end of the growing season. General field observations indicated that many spindly individuals were produced by the 3- and 4-week reapplication frequencies of 100 and 250 ppm. These observations were confirmed by the diameter measurements. Diameter growth was also reduced considerably in the 250 ppm five-week treatment and the lanolin paste treatment, and "F" values obtained for average stem diameter further substantiate these observations.

The statistical analyses of survival and root weight data are interesting because they follow a similar pattern. Significant "F" values were obtained in control *vs.* spray, levels and level x frequencies comparisons and indicate important reductions in root development and survival were produced by the higher treatments levels. Dieback of seedlings during periods of rapid growth also appears to be influenced by treatment level.

The influence of frequencies of reapplication fails to be significant when it is tested against the interaction term. In a number

TABLE 4. Analysis of variance of survival, dieback, height, diameter, and root development data.

		Source of variation					
	Total (21)[1]	Control vs. spray (1)	Lanolin vs. spray (1)	Levels (2)	Frequencies (2)	LxF interaction (4)	Error (11)
Survival							
SS	10461.3	386.0	599.1	7310.9	615.8	991.6	557.81
MS		386.0	599.1	3655.4	307.9	247.9	50.7
F		7.6*	11.8**	14.7*	1.2	4.9*	
Dieback							
SS	797.6	111.8	16.7	273.0	63.4	33.4	299.4
MS		111.8	16.7	136.5	31.7	8.4	27.2
F		4.1	0.6	5.0*	1.2	.3	
Av. Height							
SS	2549.4	14.6	250.4	108.7	286.2	532.4	1357.2
MS		14.6	250.4	54.3	143.1	133.1	123.4
F		0.1	2.0	0.4	1.2	1.1	
Av. Stem Diameter							
SS	.433	.059	.001	.166	.088	.069	.050
MS		.059	.001	.083	.043	.017	.0045
F		13.1**	0.2	4.8	2.5	3.8*	
Av. o.d. Wt. of Roots							
SS	202.7	43.7	1.1	101.7	25.7	26.5	3.9
MS		43.7	1.1	50.9	12.8	6.6	.35
F		124.8**	3.1	7.7*	1.9	18.9**	

[1]The numerals in parentheses indicate degrees of freedom.
*Significant at 5 percent level; **Significant at 1 percent level.

of cases this is due to the interaction term being highly significant. Examination of the data often shows obvious reasons. Stem diameter and ovendry weight of the roots, for example, are little influenced by the frequency of reapplication at the 250 and 10 ppm levels. At the high treatment level stem diameter and root growth are much reduced regardless of the frequency of application whereas the low level fails to influence growth significantly even when applied every three weeks. In contrast to this, at the 100 ppm level of gibberellic acid, stem and root growth appear to be very sensitive to frequencies of reapplication. This situation is reflected in the analysis of variance by a highly significant interaction term.

The 250 ppm gibberellic acid treatments at all frequencies of reapplication were characterized by greatly reduced survival, a high percentage of trees showing evidence of the dying back of the growing point, reduced diameter growth and little or no height growth response. Root development was greatly reduced. Leaves were commonly long and narrow, much reduced in total area, light yellow in color and many exhibited marginal discoloration and small scattered necrotic areas. Table 2 presents data which indicates the magnitude of the treatment effects and Figure 6 illustrates the typical reduction in root development that was observed in treated individuals at the higher treatment levels and frequencies of reapplication.

Trees in the 100 ppm three-week and the 100 ppm four-week treatments, although having much improved survival over the 250 ppm treatments, exhibited similar symptoms of overstimulation. The 100 ppm five-week treatment, although causing slightly reduced survival, greater dieback, and a somewhat reduced root system as compared with control, was the only treatment in which the treated trees exceeded the height growth and equaled the diameter growth of the control trees. Leaf size, shape and color, although slightly modified, was very similar to that of the control trees.

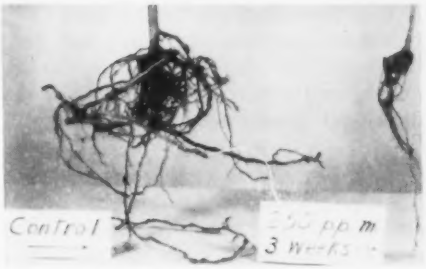


FIGURE 6. *Root development was seriously reduced, as illustrated by the above seedlings, when the higher treatment levels and more frequent reapplication frequencies were employed.*

The trees in the 10 ppm treatment, although showing a slight reduction in root development failed to differ from the control trees in leaf size, color, and growth characteristics. The trees treated with 1 percent gibberellic acid in lanolin paste survived well but failed to outgrow the control trees in height or diameter growth and exhibited a sizable decrease in root development.

Fiber measurements fail to substantiate

TABLE 5. Fiber lengths of seedlings treated with gibberellic acid.

Treatment	Fiber length in millimeters[1] Replication 1		Replication 2		Average
Control	.42	.41	.36	.39	.394
Lanolin	.44	.41	.41	.38	.410
10 ppm 3 weeks	.42	.41	.40	.36	.388
100 ppm 3 weeks	.36	.37	.38	.30	.346
250 ppm 3 weeks	.36	.35	.31	.31	.333
100 ppm 5 weeks	.36	.40	.38	.37	.378
Control (re-check)	.43	.37	.39	.37	.390

[1]Standard deviation of the mean of one treatment: .007 mm; least significant difference: .020 mm.

original hopes that height growth increases would be accompanied by increases in fiber length (Table 5). Close scrutiny of the data reveals that only the trees from the three-week treatments (both the 250 and 100 ppm) were significantly different from the control, and in these cases the fiber lengths were shorter. The trees in the 100 ppm five-week treatment, although taller than the control trees, did not differ significantly in fiber length.

Discussion

The late summer slowdown in growth of the trees in the 250 ppm treatments, and in the three- and four-week treatments with 100 ppm apparently was related to the decreased root development and the decreased total leaf area of the treated individuals. Dieback of the growing tip, greatest during periods of rapid growth and under conditions of maximum moisture stress, was most serious at the higher treatment levels. This apparently was related to decreased root development and the presence of an increased amount of succulent, rapidly growing stem tissue.

The lanolin paste treatment did not produce the response that might be expected based on the preliminary trial. The reduced growth of the trees in this treatment in part seems to be related to reduced root development. The height growth data for the trees treated with lanolin paste is difficult to interpret in relation to the other treatments because it is the result of reduced growth response, high survival, and a moderate amount of dieback; while in the case of the 250 ppm treatments, for example, the average height information listed is the result of excessive response, poor survival, and a fairly large amount of dieback. Survival was important in this latter instance because it was necessary to omit a rapidly growing tree from the measurements when it died back completely, and to base the average figure presented in the table on the remaining trees.

Data fail to show any increase in fiber length due to the treatments employed. This seems to be in conflict with the results of Swan (1958) who obtained fiber-length increases of approximately 19 percent when working with hybrid poplars treated with gibberellic acid. His fiber-length increases, however, were associated with height growth response of approximately 65 percent.

Aspen is apparently quite sensitive to dosages and frequencies of application of gibberellic acid. Evidently a fairly fine balance exists between stimulation and overstimulation. With additional work on treatment levels and frequencies of application it seems entirely possible that greater height growth response could be obtained especially if fertility levels and moisture levels are maintained at nearly optimum conditions. Examination of fiber lengths under conditions of greater growth response would doubtless give a better insight into this aspect of the problem.

Summary

A preliminary greenhouse trial and subsequent replicated field trials were carried out to study the effects of gibberellic acid on the growth and on fiber length of quaking aspen.

1. The preliminary trial, conducted for an 8-week period, indicated that gibberellic acid, applied as a spray or as a lanolin paste, affected growth under greenhouse conditions. Response was rapid and overstimulation resulted when spray treatments at concentrations of 500 ppm and 100 ppm were applied every two weeks.

2. Replicated field trials revealed that early height growth response was not as pronounced in the field as in the greenhouse. Height measurements after 8 weeks in the field indicated that seedlings treated with the higher levels of gibberellic acid (250 ppm and 100 ppm) had the greatest average seedling height. Later measurements revealed that late summer growth of the control trees was quite rapid and that there was little difference in the total height between control trees and the treated trees by the end of the growing season. The

treated seedlings in the 100 ppm 5-week treatment were the only seedlings which exceeded the control trees in average height and average diameter. The diameter growth differences for this treatment were not statistically significant.

3. Field survival after 6 weeks and at the end of the growing season was poorest in the 250 ppm treatments and greatest in the control, the 1 percent gibberellic acid in lanolin, and in the 10 ppm level.

4. Most dieback of the growing tip was observed in the higher treatment levels and the least in the control and the 10 ppm treatments.

5. Root development was best on the control trees and those in the 100 ppm 5-week treatment. Root development was greatly impaired in all treatments with 250 ppm, the 100 ppm 3-week, the 100 ppm 4-week treatments, and the gibberellic acid-lanolin paste treatment.

6. Leaf discoloration at the margins, yellowing, and the presence of necrotic spots were noted at the 250 ppm and the 100 ppm concentrations. Leaves of trees treated with gibberellic acid at higher levels were longer and narrower and had a total surface area much lower than the control and the 10 ppm concentrations. The leaf area differences along with the root development of some of the heavier treatments apparently accounted for the growth advantage of the control plants late in the summer.

7. Fiber length determinations were made on a limited number of seedlings, four sets of measurements being taken for each treatment. Seedlings from the lanolin, and the 10 ppm treatments had the longest fibers but did not differ significantly from the controls. The 100 ppm and the 250 ppm treatments when applied every three weeks, produced seedlings with significantly shorter fibers than the control. Trees from the 100 ppm 5-week treatment had fibers that were slightly shorter but not significantly different from the controls.

Literature Cited

HACSKAYLO, J., and MURPHEY, W. K. 1958. Response of 9-year old McKee hybrid poplar to gibberellic acid. Ohio Agric. Expt. Sta. Res. Circ. 54. 8 pp.

KNIGHT, H. A. W. 1958a. Gibberellic acid application to Engelmann spruce seedlings. For. Res. Rev. B. C. For. Serv. 1957/58:34-35.

———. 1958b. Gibberellic acid application to western hemlock seedlings. For Res. Rev. B. C. For. Serv. 1957/58:36-37.

MARTH, P. C., AUDIA, W. V., and MITCHELL, J. W. 1956. Gibberellic acid—a plant growth regulator. Hort. Crops Res. Branch, Agric. Res. Ser., U. S. Dept. Agric. Beltsville, Md. Mimeo. 8 pp.

NELSON, T. C. 1957. Early responses of some southern tree species to gibberellic acid. J. For. 55:518-520.

SCHAEDLE, M. 1958. Gibberellic acid application to Douglas Fir seedlings. For. Res. Rev. B. C. For. Serv. 1957/58: 35.

SPEARIN, W. E. and ISENBERG, I. H. 1947. The maceration of woody tissue with acetic acid and sodium chlorite. Science 105:214.

SWAN, H. S. D. 1958. The influence of gibberellic acid on the growth and development of hybrid poplar. Woodland Res. Index Pulp Paper Res. Inst. Can. No. 105.

WESTING, A. H. 1959. Effect of gibberellin on conifers: Generally negative. J. For. 57:120-122.

Properties of Some Random and Systematic Point Sampling Estimators

BY
MARSHALL N. PALLEY
LEAH G. HORWITZ

THE BITTERLICH method of sampling forest stands has won widespread acceptance since it was first introduced (1948). The original conception of estimating stand basal area by counting trees was extended by Grosenbaugh (1952) to provide for estimates of volume, number of trees, or other stand variables, based on measurements of the sampled trees. He showed (1958) that such sampling was done with probability proportional to size and was capable of giving unbiased estimates of means and variances. Much work remains to be done on the variance and distribution of these estimates so that meaningful confidence statements can be made, the effect of changes in the sampling angle studied, and the relative effectiveness of this method and traditional plot sampling compared for particular forests. This paper is presented as a necessary preliminary to the further consideration of these important questions. It will deal with the unbiasedness and the variance in the class of Bitterlich-type samples called point samples. Both random and systematic sampling plans will be examined. A modified version of point sampling involving a subsample described by Bell and Alexander (1957) will also be considered.

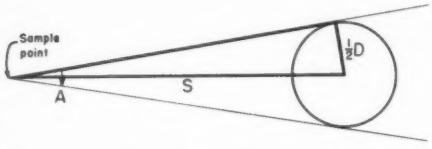


FIGURE 1. *Geometry of the point sampling rule.*

Sampling Procedure

In the Bitterlich method of drawing a sample the primary sampling unit is a cluster of trees associated with a locus of origin. The locus of origin is a point in the case of point sampling, a line in the case of line sampling, an alternative but related procedure proposed by Strand (1957). A tree is included within the cluster in point sampling if the distance, S, from the tree to the sampling point, divided by the radius of the tree, $1/2\ D$, is less than some constant value, K. The condition for including a tree in a particular sampling unit then is

$$S/\frac{1}{2}D < K$$

which may also be written as

$$\text{cosec } 1/2\ A < K$$

where A is the angle formed by lines of sight from the sampling point to the opposite edges of the tree. Figure 1 pictures the situation in the plane of the breast-height

The authors are, respectively, Lecturer in the School of Forestry, University of California, Berkeley, California; and, formerly Statistician, School of Forestry, University of California, Berkeley. Appreciation is expressed to Elizabeth L. Scott, R. Zasepa, and W. G. O'Regan for reading versions of the manuscript and making helpful suggestions. Manuscript received Jan. 3, 1960.

of the tree, 4.5 feet above the ground.

This angular relationship is the key to the simplicity of Bitterlich's proposal for distinguishing the trees associated with each sampling point. If a fixed angle α is so chosen that α is twice the angle whose cosecant is K, then a tree is selected for inclusion in the sampling unit if the angle formed by lines of sight to the edges of the tree is larger than the reference angle α. In this way, neither the distance from the sampling point to the tree nor the diameter of the tree need be measured to determine its inclusion. It will be seen that this type of sample will include more large trees and fewer small trees in the sample than their proportionate representation in the forest. In Figure 2, trees 1, 3, and 5 are included at point P, while trees 2 and 4 are not included. In practice, reference angles are small, of the order of one to four degrees. Typically a small number of trees, up to perhaps 30 in number, is associated with a sampling point.

A number of convenient instruments have been devised by Bitterlich and others for projecting the reference angle outwards from the sampling point. Some of these compensate for the effect of sloping ground. Others such as the simple hand-held glass prism, may be adapted for such special circumstances. A good summary of the instrumentation of the method is given by Finch (1957). Adjustments to take account of sloping ground and the elliptical shapes of tree cross sections are dealt with by Grosenbaugh (1958).

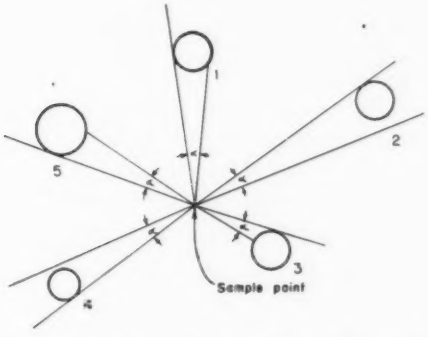


FIGURE 2. *Association of trees with a sample point.*

Assumptions and Notation

The plan in this paper is to find the expectations and variances of some of the estimators suggested for use with point sampling. The analysis which follows assumes a level forest of known extent, whose land area is denoted by L. There are N trees distributed over the forest in a fixed manner and so located that no tree center is nearer to the edge of the forest than the product of its radius, r, and a constant, K. The basal area (cross-sectional area 4.5 feet above the ground) of tree i is symbolized by b_i. The trees are all assumed to stand vertically and to be circular in cross section. There are no obstructions to visibility owing to distance or intervening vegetation. All measurements are assumed to be made without error. The size and arrangement of trees is perfectly definite and fixed. The only random elements are the locations of the sampling points making up a particular sample.

The notation which is to be used is summarized here for the convenience of the reader:

A = angle with sampling point as vertex, tangents to the tree as sides.

α = twice the angle whose cosecant is K. (cosec $\alpha/2 = K$)

K = a numerical constant

L = total land area in the forest

L/K^2 = basal area factor

r_i = radius of the ith tree

b_i = basal area of the ith tree

z_i = volume of the ith tree

$q_i = z_i/b_i$ = ratio of volume to basal area of the ith tree

N = total number of trees in the forest ($i=1,2,\ldots,N$)

$G = \sum_{i=1}^{N} b_i$ = total basal area in forest

$V = \sum_{i=1}^{N} z_i$ = total volume in the forest

n = number of points in a sample ($j = 1,2, \ldots, n$)

m = number of points in a subsample ($j = 1,2, \ldots, m$)

$p = n/m$, reciprocal of subsampling fraction; m, n and p all integers

$Y_{ij} = 1$ if ith tree included at jth sample point, zero otherwise

$N_j = \sum_{i=1}^{N} y_{ij}$ = number of trees included at the jth sample point

$g = L/K^2 n \left(\sum_{j=1}^{n} N_j \right)$ = Bitterlich's estimator for total basal area

$v = L/K^2 n \left(\sum_{j=1}^{n} \sum_{i=1}^{N} q_i y_{ij} \right)$ = Grosenbaugh's estimator for total volume

O_{hi} = area of overlap between the K-circles of the hth and ith trees

O'_{hi} = overlapping co-incident areas between the K- circles of hth and ith trees

g_f = estimator for total basal area in a systematic point sample

n' = number of points in one systematic subsample

$C = \frac{n}{n'}$ = the number of independent systematic subsamples forming one sample

$\bar{g}$ = estimator for total basal area in a systematic point sample with C random starts

The Basal Area Estimate

Bitterlich's estimator for total basal area (1948) is formed by multiplying the average number of trees included at a sample point by a constant basal area factor associated with the angle gauge used. To write an expression for this estimator we define a set of indicator random variables Y_{ij} which take on the value 1 when tree i is included at sample point j and the value 0 when it is not. At each sample point we consider every tree in the forest and ask the question: "Is this tree included at this sample point?" If it is included, we assign a value of 1 to the random variable associated with that tree and that sample point, that is, we count the tree. In a random sample of n points with the basal area factor denoted by L/K^2 the estimator for total basal area[1] may be written

$$g = \frac{L}{K^2 n} \sum_{j=1}^{n} \sum_{i=1}^{N} y_{ij} \qquad (1)$$

where y_{ij} is the value (either 0 or 1) taken on by Y_{ij}.

Sampling Properties. We wish to investigate whether g is in fact an unbiased estimator of G and whether a proposed estimator for the variance of g is an unbiased estimator of the true variance of g. It will, therefore, be necessary to find the expectation of g, the true variance of g, and the expectation of a suggested estimator for the variance of g, under the assumption that the points making up a sample are randomly and independently located.

As a step in finding the required expectations we look first at the expected value of the indicator variable Y_{ij}, the only random element in the sampling situation. Since this variable can take on only the values 0 or 1, its expectation is simply the probability that

[1]The quantity to be estimated here is conceived to be total basal area in the forest, $G = \sum_{i=1}^{N} b_i$. This is closely related to average basal area per unit area in the forest, G/L. In the latter framework the basal area may be expressed either in square feet per acre or square meters per hectare, the basal area factors being, respectively, $43{,}560/K^2$ and $10{,}000/K^2$.

it takes on the value 1, that is the probability that the ith tree will be included when the jth sample point is located at random in the forest. The area within the forest which meets the inclusion condition $S_i < Kr_i$ is the circle traced by a radius Kr_i units in length and centering on the center of the tree. This enlarged circle or ring which may be conceived to surround each tree in the forest has been termed the K-circle by Grosenbaugh (1955) and is pictured in Figure 3. In symbols we may write:

$$\begin{aligned} E(Y_{ij}) &= \Pr\,(Y_{ij} = 1)(1) \\ &\quad + \Pr\,(Y_{ij} = 0)(0) \\ &= \frac{\text{ring area of } i\text{th tree}}{\text{land area}} \\ &= \frac{\pi(Kr_i)^2}{L} = \frac{K^2 b_i}{L} \end{aligned}$$

using the relationship that $\pi r_i^2 = b_i$, the basal area of the ith tree.

This expression may be used in finding the expectation of g:

$$\begin{aligned} E(g) &= \frac{L}{K^2 n} E\left(\sum_{j=1}^{n}\sum_{i=1}^{N} Y_{ij}\right) \\ &= \frac{L}{K^2 n}\sum_{j=1}^{n}\sum_{i=1}^{N} E(Y_{ij}). \end{aligned}$$

Substituting the expected values of the Y_{ij} and summing over all trees and over the n points:

$$E(g) = \frac{L}{K^2 n}\cdot\frac{nK^2\sum_{i=1}^{N} b_i}{L} = \sum_{i=1}^{N} b_i = G.$$

Bitterlich's g is thus an unbiased estimate of G, the total basal area in the forest, under conditions of random sampling.

Variance of g: It is convenient to define $N_j = \sum_{i=1}^{N} Y_{ij}$. Then the variance of g, using the theorem on the variance of a linear combination is

$$\sigma_g^2 = \left(\frac{L}{K^2 n}\right)^2 \left\{\sum_{j=1}^{n}\sigma^2_{N_j} + 2\sum_{j=1}^{n-1}\sum_{k=j+1}^{n}\sigma_{N_j N_k}\right\} \qquad (2)$$

where $\sigma_{N_j N_k}$ is the covariance between

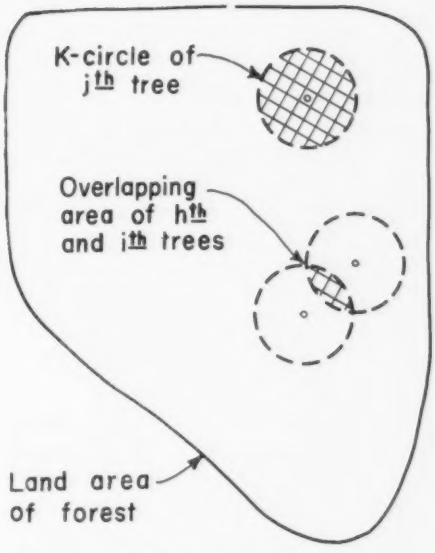


FIGURE 3. *K-circles and overlapping area.*

the tree counts at the jth and the kth points. Since the sampling is at random, all the variances of the N_j are equal and the covariances are zero. Then

$$\sigma_g^2 = \left(\frac{L}{K^2 n}\right)^2 n\sigma^2_{N_j} = \frac{L^2}{nK^4}\,\sigma^2_{N_j}.$$

Recall that, by definition

$$\sigma^2_{N_j} = \sigma^2_{\sum_{i=1}^{N} Y_{ij}} = \sum_{i=1}^{N}\sigma^2_{Y_{ij}} + 2\sum_{h=1}^{N-1}\sum_{i=h+1}^{N}\sigma_{Y_{hj}Y_{ij}}. \qquad (3)$$

Of this

$$\begin{aligned} \sigma^2_{Y_{ij}} &= E(Y^2_{ij}) - [E(Y_{ij})]^2 \\ &= \frac{K^2 b_i}{L} - \left(\frac{K^2 b_i}{L}\right)^2 \end{aligned}$$

under random sampling, because Y_{ij} being an indicator variable, $E(Y^2_{ij}) = E(Y_{ij})$.

And

$$\sigma_{Y_{hj}Y_{ij}} = E(Y_{hj}Y_{ij}) - \frac{K^4 b_h b_i}{L^2}.$$

Thus

$$\sigma^2_{N_j} = \sum_{i=1}^{N} \frac{K^2 b_i}{L} - \sum_{i=1}^{N} \frac{K^4 b^2_i}{L^2} + 2 \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} E(Y_{hj} Y_{ij}) - 2 \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} \frac{K^4 b_h b_i}{L^2}$$

which, combining the second and fourth terms, reduces to

$$\sigma^2_{N_j} = \frac{K^2}{L} \sum_{i=1}^{N} b_i - \frac{K^4}{L^2} \left(\sum_{i=1}^{N} b_i \right)^2 + 2 \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} E(Y_{hj} Y_{ij}).$$

To find $E(Y_{hj}Y_{ij})$ notice that $Y_{hj}Y_{ij} = 1$ if and only if the jth point falls in the overlap of the K-circles corresponding to the hth and ith trees. The cross-hatched area in the two-circle case illustrated in Figure 3 is this overlapping area, which will be denoted by O_{hi}. It follows that

$$E(Y_{hj} Y_{ij}) = \frac{O_{hi}}{L} .$$

Therefore

$$\sigma^2_{N_j} = \frac{K^2}{L} \sum_{i=1}^{N} b_i \left[1 - \frac{K^2}{L} \sum_{i=1}^{N} b_i \right] + \frac{2}{L} \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} O_{hi}. \qquad (4)$$

And

$$\sigma^2_g = \frac{L^2}{K^4 n} \frac{K^2}{L} G \left[1 - \frac{K^2}{L} G \right] + \frac{2}{L} \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} O_{hi} \Bigg\} = \frac{L}{K^2 n} G \left(1 - \frac{K^2}{L} G \right) + \frac{2L}{K^4 n} \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} O_{hi}. \qquad (5)$$

The variance of g is seen to be proportional to the land area and to the total basal area in the forest and to be inversely proportional to n, the sample size, as might be expected. An increase in the constant K will tend to decrease the variance of g, but this decrease may be offset by the resulting increase in the sum of the overlapping areas. The spatial distribution of the trees in particular forests will affect the nature of the change in variance accomplished by an increased value of K.

With appropriate modifications, it is possible to rewrite the expressions for estimating total basal area and the variance of total basal area so that the more general case of forests with trees near the edge may be included. The formulas reflecting the adjusted probabilities occasioned by trees whose K-circles overlap the edge of the forest are not cited here because of their added length and complexity.

It is shown in the appendix that the standard form for the variance of an estimator

$$s^2_g = \frac{L^2}{K^4 n} \left\{ \frac{n \sum_{j=1}^{n} N_j^2 - \left(\sum_{j=1}^{n} N_j \right)^2}{n(n-1)} \right\} \qquad (6)$$

is an unbiased estimate of σ^2_g. An example of the computation of s_g^2 is worked out below in connection with the discussion of the volume estimate.

The Volume Estimate

When the volume and basal area are determined for each tree included at every point in the sample, total volume may be estimated by the following expression (Grosenbaugh 1952):

$$v = \frac{L}{K^2 n} \sum_{j=1}^{n} \sum_{i=1}^{N} q_i y_{ij} \qquad (7)$$

where $q_i = \frac{z_i}{b_i}$, the ratio of volume to basal area of the ith tree and y_{ij} is the particular observed value of the random variable Y_{ij}. The same procedure used to determine the expectation of g may be used to show that v is an unbiased estimator of V, the total volume in the forest. Similarly,

$$\sigma_v^2 = \left(\frac{L}{K^2 n} \right)^2 \left\{ \sum_{j=1}^{n} \sum_{i=1}^{N} q_i^2 \sigma^2_{y_{ij}} + 2 \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} q_h q_i \sigma_{y_{hj} y_{ij}} \right\} \qquad (8)$$

$$= \frac{L^2}{K^4 n} \left\{ \frac{K^2}{L} \sum_{i=1}^{N} q^2_i b_i - \frac{K^4}{L^2} \left(\sum_{i=1}^{N} q_i b_i \right)^2 + \frac{2}{L} \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} q_h q_i O_{hi} \right\}$$

The unbiased estimate of this variance is

$$s_v^2 = \frac{L^2}{K^4 n} \times \left\{ \frac{n \sum_{j=1}^{n} \left(\sum_{i=1}^{N} q_i y_{ij} \right)^2 - \left(\sum_{j=1}^{n} \sum_{i=1}^{N} q_i y_{ij} \right)^2}{n(n-1)} \right\}. \quad (9)$$

Computations. A numerical example will show the computations needed to estimate volume and basal area and the variance of volume and basal area estimates under random sampling. The data given in Table 1 are taken from some point sampling trials conducted by Cox in mixed conifer stands on the Latour State Forest, California.[2] For each of 44 sampling points the number of trees included, N_j, and the sum of the volume to basal area ratios for these trees, $\sum_{i=1}^{N} q_i y_{ij}$, is listed. Other terms needed are computed from the data in Table 1 as follows:

$$\sum_{j=1}^{44} N_j^2 = 9^2 + 9^2 + 7^2 + \ldots + 17^2 = 10{,}259$$

$$\sum_{j=1}^{44} \left(\sum_{i=1}^{N} q_i y_{ij} \right)^2 = 2228^2 + 1896^2 + \ldots + 3027^2 = 358{,}471{,}162$$

The value of L/K, the basal area factor on a per acre basis, is given as 9.372. Using formulas presented above, the following estimates[3] are obtained.

Basal area per acre:

$$g_a = \frac{9.372}{44} \cdot 617 = 131.42 \text{ sq. ft.}$$

Volume per acre:

$$v_a = \frac{9.372}{44} \cdot 112{,}832 = 24{,}033 \text{ bd.ft.}$$

[2]Data kindly provided by Paul Cox, California State Division of Forestry.

[3]The symbols g_a and v_a stand for estimates of basal area and volume on a per acre basis; $s_{g_a}^2$ and $s_{v_a}^2$ are the estimated variances of basal area per acre and volume per acre.

TABLE 1. Tree count and sum of ratios at 44 sampling points, Latour State Forest.

Sample Pt. j	No. trees included N_j	Sum of ratios $\sum_{i=1}^{N} q_i y_{ij}$
1	9	2228
2	9	1896
3	7	991
4	14	2737
5	19	2899
6	17	2560
7	16	3469
8	21	4746
9	10	2048
10	21	5762
11	11	1649
12	16	2798
13	25	4466
14	17	3343
15	12	3230
16	22	3067
17	18	3658
18	9	1685
19	18	4268
20	11	3344
21	3	609
22	5	793
23	10	958
24	10	1789
25	12	2144
26	6	1021
27	18	3710
28	18	3134
29	11	1299
30	1	284
31	8	1329
32	5	688
33	19	3000
34	15	2646
35	11	1835
36	19	2661
37	24	4258
38	23	3225
39	11	1818
40	8	1192
41	19	2486
42	25	4860
43	17	3222
44	17	3027
Totals 44	617	112,832

Variance of the estimate of basal area:

$$s^2_{g_a} = \frac{(9.372)^2}{44} \frac{44(10{,}259) - (617)^2}{44 \cdot 43}$$
$$= 74.60$$

Variance of volume:

$$s^2_{v_a} = \frac{(9.372)^2}{44} \times \frac{44(358{,}471{,}162) - (112{,}832)^2}{44 \cdot 43}$$
$$= 3{,}209{,}246$$

Volume estimate of Bell and Alexander. Bell and Alexander (1957) have proposed a modified procedure for estimating volumes in which the number of trees N_j, included at a sampling point is determined at all the sample points, but the sum of volume to basal area ratios is determined at only a fraction of the sample points. Their estimator for total volume may be written

$$v' = \frac{L}{K^2 n} \cdot \frac{\sum_{j=1}^{n} N_j}{\sum_{j=1}^{m} N_j} \cdot \sum_{j=1}^{m} \sum_{i=1}^{N} q_i y_{ij} \quad (10)$$

where n = the total number of sample points and m is the number of points at which sums of ratios are found. A numerical example showing the computation of v' is given below in connection with the computation of the mean square error of v'.

Sampling properties of v': The characteristics of v' are investigated under the assumption of random sampling. Multiplying both numerator and denominator of (10) by L/K^2m gives

$$v' = \frac{\frac{L}{K^2 m} \sum_{j=1}^{m} \sum_{i=1}^{N} q_i y_{ij}}{\frac{L}{K^2 m} \sum_{j=1}^{m} N_j} \cdot \frac{L}{K^2 n} \sum_{j=1}^{n} N_j$$
$$= \frac{v}{g} \cdot g'$$

in which v and g are the estimates formed from the subsample and g' is the estimate of basal area based on the total sample. Bell and Alexander's v' is seen in this form to be a ratio estimate. Following Hansen, Hurwitz and Madow (1953, vol. II, Chap. 4) the expectation of v' and its mean square error are:

$$E(v') = V \times \left\{1 + \frac{\sigma_{v,g'}}{VG} - \frac{\sigma_{v,g}}{VG} + \frac{\sigma^2_g}{G^2} - \frac{\sigma_{g,g'}}{G^2}\right\} \quad (11)$$

and

$$\text{M.S.E.}(v') = V^2 \left\{\frac{\sigma^2_v}{V^2} + \frac{\sigma^2_{g'}}{G^2} + \frac{\sigma^2_g}{G^2} + \frac{2\sigma_{v,g'}}{VG} - \frac{2\sigma_{v,g}}{VG} - \frac{2\sigma_{g,g'}}{G^2}\right\}. \quad (12)$$

The variances and covariances linking the large and small samples are as follows:

$$\sigma^2_{g'} = \frac{1}{p}\, \sigma^2_g$$
$$\sigma_{g,g'} = \frac{1}{p}\, \sigma^2_g$$
$$\sigma_{v,g'} = \frac{1}{p}\, \sigma_{v,g}$$

where the integer $p = n/m$. These relationships are derived in the Appendix. The expression for the expectation of v' (11) indicates that it is a biased estimator of total volume. Making use of the variance and covariance relationships linking the main and the subsamples, this bias may be written as

$$E(v' - V) = V\left(\frac{p-1}{p}\right)\left(\frac{\sigma^2_g}{G^2} - \frac{\sigma_{vg}}{VG}\right) \quad (13)$$

or in terms of the correlation coefficient between v and g, $\rho_{v,g}$:

$$E(v' - V) = V\left(\frac{p-1}{p}\right)\left(\frac{\sigma^2_g}{G^2} - \frac{\rho_{v,g}\sigma_v\sigma_g}{VG}\right)$$
$$= V\left(\frac{p-1}{p}\right)\frac{\sigma_g}{G}\left(\frac{\sigma_g}{G} - \frac{\rho_{v,g}\sigma_v}{V}\right). \quad (14)$$

This form of the expression for the bias indicates that if

$$\rho_{v,g} \cong \frac{\sigma_g/G}{\sigma_v/V}$$

the bias of v' is sure to be small.

Because of the bias of the ratio estimate v', we work with the mean square error of v' rather than with its variance. The

expression for the mean square error of v' (12) may be written:

$$\text{M.S.E.}(v') = V^2 \left\{ \frac{\sigma_v^2}{V^2} + \frac{\frac{1}{p}\sigma_g^2}{G^2} + \frac{\sigma_g^2}{G^2} + \frac{\frac{2}{p}\sigma_{v,g}}{VG} - \frac{2\sigma_{v,g}}{VG} - \frac{\frac{2}{p}\sigma_g^2}{G^2} \right\}$$

and combining terms further

$$\text{M.S.E.}(v') = V^2 \left\{ \frac{\sigma_v^2}{V^2} - \frac{2(p-1)}{p} \frac{\sigma_{v,g}}{VG} + \frac{p-1}{p} \frac{\sigma_g^2}{G^2} \right\}.$$

In relative terms, we may write:

$$\frac{M.S.E.(v')}{V^2} = \frac{\sigma_v^2}{V^2} - \frac{p-1}{p} \left(\frac{2\sigma_{v,g}}{VG} - \frac{\sigma_g^2}{G^2} \right) \quad (15)$$

It follows from this expression that there will be no advantage in using v' rather than v whenever, in terms of the correlation coefficient,

$$2\rho_{v,g} < \frac{\sigma_g/G}{\sigma_v/V}.$$

In order to make an informed choice between a single sampling plan to estimate volume using v and a double sampling plan using v', a knowledge of the relative costs of counting trees and measuring their volumes and basal areas is needed, as well as some information on the variances and covariances in the particular forest under consideration.

In order to estimate the relative error of v', we follow the suggestion of Hansen, Hurwitz and Madow (1953, vol. I, p. 176). The simplest estimator of this relative error follows directly upon Equation (15):

$$\frac{s^2(v')}{v'^2} = \frac{s_v^2}{v'^2} - \frac{p-1}{p} \left(\frac{2s_{v,g}}{vg} - \frac{s_g^2}{g^2} \right). \quad (16)$$

The necessary estimates of variances, covariances, volume and basal area are based on the subsample. The large sample is used only for the estimate of volume, v'. Table 2 gives the numbers of trees included at each of 44 additional sample points on the

TABLE 2. Tree count at 44 additional sampling points, Latour State Forest.

Sample Pt. j	No. trees included N_j
45	19
46	19
47	12
48	22
49	14
50	12
51	11
52	10
53	12
54	25
55	10
56	9
57	9
58	6
59	9
60	16
61	7
62	9
63	9
64	7
65	13
66	6
67	14
68	10
69	19
70	22
71	16
72	9
73	9
74	8
75	2
76	24
77	4
78	10
79	31
80	24
81	13
82	14
83	10
84	24
85	25
86	22
87	21
88	20
Total	617

Latour State Forest. The 44 points given in Table 1 are considered to be the subsample, the 88 points listed in Tables 1 and 2 to be the large sample in a numerical example illustrating the computation of v' and of $s^2(v')/v^2$. In terms of sample size we have $n = 88$, $m = 44$, and $p = 2$. The estimate of volume by Equation (10) is

$$v'_a = \frac{9.372}{88} \cdot \frac{1234}{617} \cdot 112{,}832 = 24{,}033 \text{ bd. ft.}$$

We note that in this particular case $v' = v$, because it happened that in the example chosen the number of trees included at 88 points was exactly twice the number included at 44.

To estimate the mean square error of v' we make use of the quantities computed for the numerical illustration given above. In addition, we need the estimated covariance of v and g based on the data given in Table 1 and the total number of trees included at sample points 45-88 of Table 2. An unbiased estimate of the covariance of v and g is:

$$s_{v,g} = \frac{L^2}{K^4 m} \cdot \frac{m \sum_{j=1}^{m} \left(\sum_{i=1}^{N} q_i y_{ij} \right) (N_j)}{m(m-1)} - \frac{\sum_{j=1}^{m} \sum_{i=1}^{N} q_i y_{ij} \sum_{j=1}^{m} N_j}{m(m-1)} \qquad (17)$$

Referring to Table 1, note that

$$\sum_{j=1}^{m} \left(\sum_{i=1}^{N} q_i y_{ij} \right) (N_j) = (2228)(9) + (1896)(9) + \ldots + (3027)(17) = 1{,}875{,}118.$$

We have then

$$s_{v,g_a} = \frac{(9.372)^2}{44} \cdot \frac{(44)(1{,}875{,}118) - (112{,}832)(617)}{44 \cdot 43} = 13{,}596.38$$

and by (16)

$$\frac{s^2(v')}{v^2} = \frac{3{,}209{,}227.9}{(24{,}033.22)^2} - \left[\frac{2-1}{2}\right] \left[\frac{(2)(13{,}596.38)}{(24{,}033.22)(131.42)} - \frac{74.585}{(131.42)^2}\right]$$

$$= 0.0055562 - \frac{1}{2}[2(0.0043048) - (0.0043185)] = 0.0034106.$$

In percentage terms, in the illustration given

$$\frac{s(v')}{v} \cdot 100\% = \sqrt{0.0034106} \cdot 100\% = 5.8\%$$

based on 88 points and a subsample of 44, compared with

$$\frac{s(v)}{v} \cdot 100\% = \sqrt{0.0055562} \cdot 100\% = 7.5\%$$

based on just the 44 points without the use of double sampling.

The proposal which is offered by Bell and Alexander (1957, p. 17) for estimating the relative error $s(v')/v$ can only be thought of as an approximation. It consists of two terms, one of which is closely related to $s(g)/g$, the other of which expresses the relative error of *tree* ratios with respect to the average of tree ratios. There is a confusion here, since in point sampling, the measurement we are concerned with attaches to points (i.e. the sum of the tree ratios at a point) rather than to trees. The formula for the relative error presented above (16) is offered as being conceptually sounder than the expression of Bell and Alexander. The subsampling fraction and the effect of the covariance between v and g are explicitly recognized.

Systematic Sampling

To this point the discussion has assumed that random sampling is followed. We now consider the effect on the foregoing analysis of drawing the points making up a sample in a systematic way. This extension of the argument is appropriate because of the widespread application of systematic

forest sampling in practice.

Specificially, we wish to investigate the estimation of total basal area under conditions of systematic point sampling with a single random start. The origin of a systematic sample of n points may be any point within the forest. The other $n-1$ points of the sample are related to the initial point in the following manner: the second point is p units distant from the first, and its orientation with respect to the first point is in a direction which is drawn at random. This direction defines the orientation of a rectilinear grid coextensive with the forest and with points p units apart in one direction and q units apart in the direction normal to that first drawn. Points are located at the intersections of this grid outwards to the forest edges until the required number n has been located. It is assumed that p and q are chosen large enough that a given tree will not be selected more than once in any given systematic sample. A systematic sample of n points drawn in this fashion may be thought of as a random sample of size one out of an infinite number of possible systematic samples.

As in the random sampling case, we construct the random variable Y_{fi} which is capable of taking on only two values: $y_{fi} = 1$ if the ith tree is included in the fth systematic sample and $y_{fi} = 0$ otherwise.

The probability that tree i will be included in any systematic sample will be n times the ratio of the area its K-circle to the total land area of the forest. That is:

$$P(Y_{fi} = 1) = \frac{nK^2 b_i}{L}.$$

For each systematic sample, an estimator for total basal area is:

$$g_f = \frac{L}{K^2} \frac{1}{n} \sum_{i=1}^{N} y_{fi},$$

which corresponds with g used previously in the random sampling case (1). The estimator for total basal area under systematic sampling is unbiased:

$$E(g_f) = \frac{L}{K^2} \frac{1}{n} \sum_{i=1}^{N} E y_{fi} = \frac{L}{K^2} \frac{1}{n}.$$

$$\sum_{i=1}^{N} n \frac{K^2 b_i}{L} = \sum_{i=1}^{N} b_i = G.$$

The variance of g_f may be found using the identity

$$\sigma g_f^2 = E(g_f^2) - [E(g_f)]^2.$$

The first term may be expanded as follows:

$$E(g_f^2) = \frac{L^2}{K^4 n^2} E\left(\sum_{i=1}^{N} y_{fi}\right)^2$$

$$= \frac{L^2}{K^4 n^2} \left\{ \sum_{i=1}^{N} E y_{fi}^2 + 2 \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} E y_{fi} y_{fh} \right\}.$$

The indicator variable $y_{fi}y_{fh}$ takes on the value 1 when trees i and h are both included in systematic sample f, otherwise 0. It is not necessary that both be included at the same sampling point, only that each one be taken in at one of the n sampling points making up the systematic sample. The probability that two particular trees will be included in a systematic sample may be visualized in the following manner. Consider a rectangular grid whose sides equal the spacing of sample points in the system and let the grid be superimposed on the forest in such a way that the K-circle of tree h lies completely within one rectangle, as pictured in rectangle 3 of Figure 4. Then consider the K-circle of

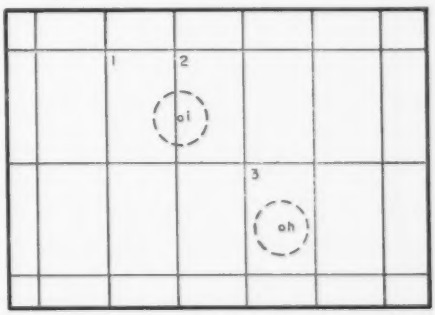


FIGURE 4. *Systematic sampling grid in relation to two representative trees.*

tree i which lies partly in rectangle 1 and partly in rectangle 2. Conceptually pick up rectangles 1 and 2 and make them coincide with rectangle 3 in the manner represented in Figure 5. The area common to the K-circle of tree h and the imposed portions of the K-circle of tree i is termed the "overlapping co-incident area" and denoted by O'_{hi}. The sum of this overlapping co-incident area in relation to the total land area of the forest is the probability that two trees will be selected at a point of the systematic sample.

$$E(y_{ni}y_{nh}) = Pr[y_{ni}y_{nh} = 1] = \mathrm{n} \cdot \frac{O'_{hi}}{L}.$$

Using this expectation in the equation above we have

$$E(gf^2) = \frac{L^2}{K^4 n^2} \left\{ \sum_{i=1}^{N} \frac{nK^2 b_i}{L} + 2 \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} \frac{O'_{hi}}{L} \cdot n \right\}$$

and

$$\sigma gf^2 \text{ syst} = \frac{L}{K^2 n} \sum_{i=1}^{N} b_i - \sum_{i=1}^{N} b_i \Bigg)^2 + \frac{2L}{K^4 n} \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} O'_{hi}.$$

Thus, we may write an expression for the true variance of the estimate formed under systematic sampling. We know of no unbiased estimator for this variance, but it may be useful to compare it term by term with the corresponding expression for random point sampling. We may rewrite the variance of a random point sample estimate (5):

$$\sigma^2(g) \text{ random} = \frac{L}{K^2 n} \sum_{i=1}^{N} b_i - \frac{1}{n} \left(\sum_{i=1}^{N} b_i \right)^2 + \frac{2L}{K^4 n} \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} O_{hi}.$$

Note that the first term is common to both expressions and that the negative term in the expression for systematic sampling variance is n times greater than the corresponding term in the random sampling variance. The overlapping area term, however, will always be larger for systematic sampling because co-incident overlaps at different points are considered as well as direct overlaps at single points. We can make no general statement about the relative magnitude of the two variances because we do not know the effect of the spatial arrangement of trees or the size of the overlapping area terms. A disturbance may be introduced into an attempt to estimate the variance of the systematic sampling estimator if there should be an unforeseen periodic distribution of variability in phase with the systematic sampling pattern.

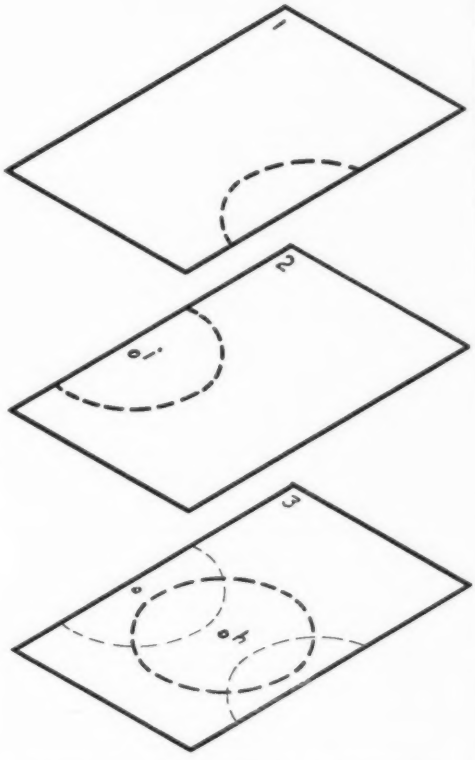


FIGURE 5. *The concept of overlapping co-incident area.*

To guard against such a possibility and to help assure an estimator with lower variance under systematic sampling, consider an alternative plan of systematic sampling with C random starts, C being a simple integer of the order of 3 or 4. Each of the systematic samples now contains n' points, the total number of points in the sample being the same as with a single start, $n = Cn'$. The spacing of points is Cp and of lines Cq, compared with the p and q of the single random start case. The orientation of the first systematic sample governs that of the remaining samples. The estimator for total basal area, g, is now the mean of the estimates provided by the C samples:

$$\bar{g} = \frac{1}{C} \sum_{f=1}^{C} g_f = \frac{1}{C} \frac{L}{K^2 n'} \sum_{i=1}^{N} \sum_{f=1}^{C} y_{fi}.$$

It differs from the g of random sampling only in the manner of selection of the points. We may show that it is unbiased:

$$E(\bar{g}) = \frac{1}{C} \frac{L}{K^2 n'} \sum_{f=1}^{C} \sum_{i=1}^{N} E(Y_{fi}) =$$

$$\frac{1}{C} \frac{L}{K^2 n'} \sum_{f=1}^{C} \sum_{i=1}^{N} \frac{K^2 b_i}{L} \quad n'$$

$$= \frac{1}{C} \sum_{f=1}^{C} \sum_{i=1}^{N} b_i = G.$$

Its variance is given by

$$\sigma^2(\bar{g}) = \frac{L}{K^2 C n'} \sum_{i=1}^{N} b_i - \frac{1}{C}$$

$$(\sum_{i=1}^{N} b_i)^2 + \frac{2L}{K^4 C n'} \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} O'_{hi}.$$

We note that this expression is valid also for the limiting cases of random sampling, setting $C = n$ and $n' = 1$, and for systematic sampling with a single start, that is, $C = 1$ and $n' = n$. The unbiased estimator for this variance is

$$s^2(\bar{g}) = \frac{1}{C} \sum_{f=1}^{C} \frac{(g_f - \bar{g})^2}{C-1}$$

$$= \frac{L^2}{K^4 C^2 n'^2} \left\{ \frac{C}{C-1} \sum_{f=1}^{C} (\sum_{i=1}^{N} y_{fi})^2 - \right.$$

$$\left. \frac{1}{C-1} \left(\sum_{f=1}^{C} \sum_{i=1}^{N} y_{fi} \right)^2 \right\}.$$

Since C is a small number, this estimator tends to have high variance. We may therefore alternatively compute $s^2(g)$, random, as an approximation to the desired variance and argue that the taking of additional systematic samples has rendered it unlikely that we will underestimate the variance of systematic sampling when we treat it as though it were random.

The same approach may be applied with necessary changes in the expressions to the estimation of total volume, using systematic sampling.

Summary

We have shown that estimators g, $\bar{g}_f$, and $\bar{\bar{g}}$ which have been proposed for basal area in random and systematic point sampling are unbiased; and similarly that the corresponding estimates for volume are unbiased. We have seen that the estimate for volume, v', formed by sampling for basal area at n points and sub-sampling for volume at a smaller number of m points out of n is biased, but with the bias small when specified relationships hold for basal area and volume parameters.

Expressions for the true variances of g and $\bar{g}$ have been derived and it has been shown that unbiased estimates of these variances s_g^2 and $s_{\bar{g}}^2$ exist, and similarly with the corresponding variances for volume. The mean square error of v' has been derived and an estimator for this mean square error has been suggested.

The conditions under which sub-sampling for volume is likely to be advantageous have been formulated. A procedure for doing systematic point sampling based on several random starts has been suggested whereby some of the advantages of both systematic and random sampling may be retained.

Supplementary Discussion

Appendix 1. Unbiased estimator for the true variance of total basal area under random point sampling:

In this appendix we demonstrate that Grosenbaugh's estimator for variance of to-

tal basal area is an unbiased estimator of the true variance. We evaluate the expectation of s_g^2, formula (6), and compare it with σ_g^2, formula (5). The expectation we are seeking is:

$$Es^2_g = \frac{L^2}{K^4 n} E\left\{ \frac{n \sum_{j=1}^{n} N_j^2 - \left(\sum_{j=1}^{n} N_j \right)^2}{n(n-1)} \right\}. \qquad (18)$$

First, we find the expectation of N_j and of N_j^2, using the definition $N_j = \sum_{i=1}^{N} Y_{ij}$:

$$EN_j = \sum_{i=1}^{N} EY_{ij} = \frac{K^2}{L} \sum_{i=1}^{N} b_i = \frac{K^2}{L} G$$

as shown above in the derivation of formula (1); and

$$EN_j^2 = E\left(\sum_{i=1}^{N} Y_{ij} \right)^2 = E\left(\sum_{i=1}^{N} Y^2_{ij} + 2 \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} Y_{hj} Y_{ij} \right)$$

as seen in the development of formula (4) above. To find the expectation of $(\sum_{j=1}^{n} N_j)^2$ we square the sum and take the expectation of the cross-products, remembering that N_j and N_k are independent:

$$E\left(\sum_{j=1}^{n} N_j \right)^2 = E\left(\sum_{j=1}^{n} N_j^2 + 2 \sum_{j=1}^{n-1} \sum_{k=j+1}^{n} N_j N_k \right)$$

and

$$EN_jN_k = E\left(\sum_{i=1}^{N} Y_{ij} \right)\left(\sum_{i=1}^{N} Y_{ik} \right) = \left(\frac{K^2}{L} \sum_{i=1}^{N} b_i \right)^2 = \frac{K^4}{L^2} G^2.$$

Then, summing and substituting into equation (18) we have:

$$Es_g^2 = \frac{L^2}{K^4 n^2 (n-1)} \left\{ n^2 EN_j^2 - nEN_j^2 - n(n-1) EN_jN_k \right\}$$

$$= \frac{L^2}{K^4 n} (EN_j^2 - EN_jN_k)$$

$$= \frac{L^2}{K^4 n} \left(\frac{K^2}{L} G + \frac{2}{L} \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} O_{hi} - \frac{K^4}{L^2} G^2 \right),$$

which is equivalent to σ_g^2, the formula for the true variance (5).

Appendix 2. Evaluation of terms in the expression for mean square error of v':

Following Hansen, Hurwitz and Madow (1953), vol. 1, p. 514) a good approximation for the mean square error of v' is

$$\text{M.S.E.}\ (v') = V^2 \left\{ \frac{\sigma_v^2}{V^2} + \frac{\sigma_{g'}^2}{G^2} + \frac{\sigma_g^2}{G^2} + \frac{2\sigma_{vg'}}{VG} - \frac{2\sigma_{vg}}{VG} - \frac{2\sigma_{gg'}}{G^2} \right\}.$$

Expressions for σ^2_g and σ^2_v are given above (5), (8). Similarly, the covariance of v and g may be written

$$\sigma_{v,g} = \frac{L}{K^2 m} \sum_{i=1}^{N} z_i b_i - \frac{1}{m} \left(\sum_{i=1}^{N} z_i \right) \left(\sum_{i=1}^{N} b_i \right) + \frac{L}{K^4 m} \sum_{h=1}^{N-1} \sum_{i=h+1}^{N} O_{hi}(q_h + q_i).$$

The variances and covariances involving g', the estimate of basal area based on the large sample of size n, may be expressed in terms of those for the small sample of size m, since $n = mp$, p being an integer:

$$g' = \frac{L}{K^2} \frac{1}{mp} \sum_{j=1}^{mp} \sum_{i=1}^{N} y_{ij}$$

$$= \frac{L}{K^2} \frac{1}{mp} \sum_{j=1}^{m} \sum_{i=1}^{N} y_{ij} + \sum_{j=m+1}^{2m} \sum_{i=1}^{N} y_{ij} + \ldots + \sum_{j=(p-1)(m+1)}^{mp} \sum_{i=1}^{N} y_{ij}.$$

Each term of this sum is of the form g/p. The variance of this sum of p independent terms is

$$\sigma^2(g') = \frac{1}{p^2} \cdot p\sigma^2_g = \frac{\sigma^2_g}{p}.$$

In finding the covariances, use is made of the theorem that cov $a(b+c)$ = cov (ab) + cov (ac):

$$\operatorname{cov}(gg') = \operatorname{cov}\left(\frac{L}{K^2}\,\frac{1}{mp}\sum_{j=1}^{mp}\sum_{i=1}^{N} y_{ij} \;\middle)\right.$$
$$\left.\frac{L}{K^2}\,\frac{1}{m}\sum_{j=1}^{m}\sum_{i=1}^{N} y_{ij} \;\right)$$
$$= \operatorname{cov}\left(\frac{L}{K^2}\,\frac{1}{mp}\sum_{j=1}^{m}\sum_{i=1}^{N} y_{ij} \;\middle)\right.$$
$$\left.\frac{L}{K^2}\,\frac{1}{m}\sum_{j=1}^{m}\sum_{i=1}^{N} y_{ij}\right.$$
$$+ \operatorname{cov}\left(\frac{L}{K^2}\,\frac{1}{mp}\sum_{j=m+1}^{2m}\sum_{i=1}^{N} y_{ij} \right)$$
$$\frac{L}{K^2}\,\frac{1}{m}\sum_{j=1}^{m}\sum_{i=1}^{N} y_{ij}$$

+ other covariances of this form.

All the covariances but the first are zero, since the others are based on a different random set of points and the associated measurements are independent of one another. It follows that

$$\sigma_{gg'} = \frac{1}{p}\,\sigma^2_g$$

and, by the same argument, it can be shown that

$$\sigma_{vg'} = \frac{1}{p}\,\sigma_{vg}.$$

Literature Cited

BELL, JOHN F. and LUCIEN B. ALEXANDER. 1957. Application of the variable plot method of sampling forest stands. Ore. Bd. For. Res. Note No. 30, 22 pp.

BITTERLICH, W. 1948. Die Winkelzählprobe. Allg. Forst-u. Holzw. Ztg. 59: 4-5. Original not consulted. Abstracted in For. Abstracts. 10: 2314. 1949.

COCHRAN, WILLIAM G. 1953. Sampling techniques. John Wiley and Sons, New York. 330 pp.

FINCH, H. D. S. 1957. Plotless enumeration with angle gauges. Forestry 30: 173-192.

GROSENBAUGH, L. R. 1952. Plotless timber estimates—new, fast, easy. J. For. 50:32-37.

————. 1955. Better diagnosis and prescription in southern forest management. Sth. For. Exp. Sta., Occasional Paper 145, 27 pp.

————. 1958. Point-sampling and line-sampling: probability theory, geometric implications, synthesis. Sth. For. Exp. Sta., Occasional Paper 160, 34 pp.

HANSEN, MORRIS H., WILLIAM N. HURWITZ and WILLIAM G. MADOW. 1953. Sample survey methods and theory. 2 vols. John Wiley and Sons, New York. 638 and 332 pp.

STRAND, LARS. 1957. "Relaskopisk" hoyde-og kubikkmassebestemmelse. Norsk Skogbr. 3:535-538.

Organic Layers in Minnesota Aspen Stands And their Role in Soil Improvement

BY
JOSEPH H. STOECKELER

QUAKING ASPEN (*Populus tremuloides* Michx.) a post-fire pioneer species, is the most widely distributed broadleaf tree species found in North America. In the three Lake States, it occupies about 19.8 million acres of land, or approximately 39 percent of the total forest area (Chase 1947). It is especially prevalent on burned-over upland forest soils formerly occupied by pine or northern hardwoods. Although not as valuable as pine or the northern hardwoods, it is important economically and is now the leading pulpwood species in this region, supplying about one-third of the total annual cut (Horn 1950). Formerly considered a weed species, aspen now occupies a significant position in the production of fiber, lumber, and specialty products.

Less appreciated is the important role of the species as a soil improver, and as a pioneer crop preceding the establishment of later more valuable stages of more tolerant sub-climax and climax types, notably balsam fir (*Abies balsamea* (L.) Mill.), and northern hardwoods, such as sugar maple (*Acer saccharum* Marsh.). This paper will document the role of aspen as a soil improver after forest fires, particularly its role in redistributing nitrogen to the surface layers, whose nutrient status is vitally important in ecological succession.

Daubenmire (1953) found aspen foliage to have the highest nutrient analysis of any of 12 western tree species studied, leading all others in average content of total nitrogen and potash, and being second in phosphorous and calcium content.

Alway and Rost (1928) came to the conclusion that forest fires were detrimental in upsetting the overall nutrient balance, since severe burns can destroy all or much of the organic layer, ranging from 7 to 26 tons per acre of oven-dry material, and representing a loss of nitrogen of 450 to 1500 pounds per acre. The mineral soil itself was not appreciably affected by burning, being only .02 percent lower in nitrogen content than unburned areas. Rowe (1953) states that intense fires may consume the entire humus layer and reduce vigor of aspen suckers.

In connection with a study of soil properties and site index of aspen in northern Minnesota and Wisconsin (Stoeckeler 1960), there was opportunity to make observations on the weight of organic layers of quaking aspen stands and to assess the role of aspen as an improver of the surface layers, especially with reference to nitrogen. Nitrogen appears to be the nutritional key in advancing plant succession toward more valuable climax types in the Lake States.

Paper No. 3969, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota. Manuscript received Mar. 16, 1960.

This report is based on a thesis submitted to the University of Minnesota, in partial fulfillment of the requirements for the Ph.D. degree. The author is indebted to C. O. Rost, retired head of the Department of Soils, and to W. P. Martin, currently head of that department at the University of Minnesota for helpful suggestions in planning and execution of the experiment and for review of the manuscript.

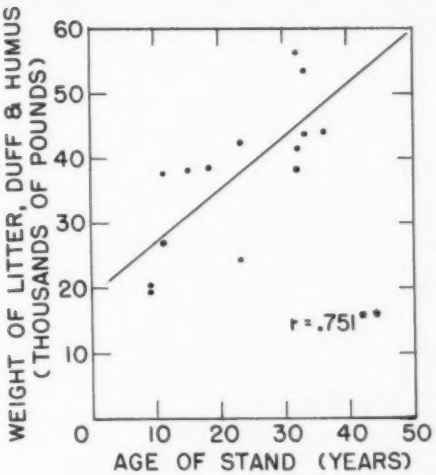


FIGURE 1. *Oven-dry weight per acre of combined litter, duff, and humus of 14 Minnesota plots as related to age of stand.*

Study Methods

Separate fractions of the organic layers in 29 quaking aspen stands in nothern Minnesota were sampled by laying out from 3 to 6 sampling areas 6 by 6 inches in size. These were sharply defined by a steel frame 4 inches high. Samples of F and H layers were kept separate. On 14 plots the L layer was also sampled. The L layer was defined as recent undecomposed leaf fall, F as a partially decomposed litter where the leaves were as yet not fully decomposed, and H as the layer of well decomposed litter not recognizable as to origin (Hoover and Lunt 1952).

Sticks,. stones and large roots were removed and the samples placed in numbered bags, later spread out at room temperature to air dry thoroughly. Once air dried, the samples were weighed, a small portion oven-dried, and the air-dry weight recalculated on an oven-dry weight basis. These data were evaluated by correlation analysis (Snedecor 1937).

The mineral portion of 21 of the profiles was sampled by horizons, five of which were sampled in detail for total nitrogen analysis. Total nitrogen was determined by the Kjeldahl method (A.O.A.C. 1950); cation-exchange capacity and replaceable bases by the method of Chapman and Kelly (1930); available phosphorous was determined by the Truog method (1930); and, pH was determined electrometrically with the Beckman pH meter.

Site index was determined by sampling from 5 to 7 representative trees of the dominant and codominant class for total height and age, and predicting all sites to age 50, using curves developed by Kittridge and Gevorkiantz (1929). Volume data were calculated from tables prepared by Gevorkiantz and Olsen (1955).

Weight of Organic Layers

The combined oven-dry weight per acre of all organic layers varied from 19 to 56 thousand pounds (Fig. 1). Based on the average line, the values for 10-year periods from the 10th to the 40th year are approximately 27, 35, 43, and 52 thousand pounds, respectively. Projecting the line back a few years to zero age, it would intersect at about 19 thousand pounds. This indicates that on the average these plots had probably almost 10 tons of oven-dry material present at time of establishment of the aspen stand. This weight of organic

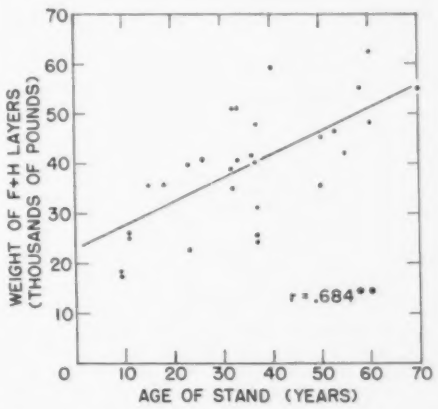


FIGURE 2. *Oven-dry weight per acre of combined* F + H *layers of 29 Minnesota plots as related to age of stand.*

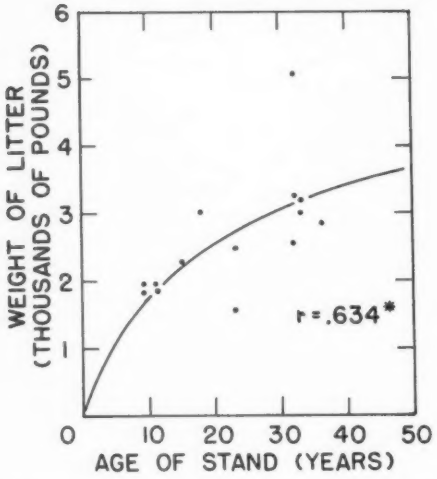


FIGURE 3. *Oven-dry weight per acre of litter layer of 14 Minnesota plots as related to age of stand. This represents essentially the annual litter fall.*

matter was hence left from the previous stand of pine, hardwood, or balsam fir-spruce after it had burned.

On 29 plots where only the weight of F and H layers was determined, the values ranged from about 17 to 62 thousand pounds. The residual amount of these layers at zero age of the aspen was about 23 thousand pounds (Fig. 2), or in close agreement with the more limited sample from 14 plots (Fig. 1).

The weight of the litter only, for 14 plots, shows an increase at least to age 35 (Fig. 3). Based on the curve values, the plots approximately 33 years old had about 3200 pounds per acre of litter, while in 10-year-old stands it was slightly over half that amount. There is some evidence that it tends to level off gradually.

The weight of F layers observed in 29 plots, ranging from 9 to 70 years, shows a substantial increase with age (Fig. 4).

The H layer has a very similar trend (Fig. 5), but the amount is substantially heavier, constituting as much as 70 to 90 percent of the entire combined weight of the Ao. Here again, there is evidence that the residue from the previous stand was largely H layer and that it must have been about 17 thousand pounds per acre.

There is apparently a rather high percent of the organic layers which becomes completely decomposed or is incorporated into the soil by the action of fungi and other soil micro-organisms. The combined organic layer production curve (Fig. 1) shows an apparent gain of some 16.5 thousand pounds in weight between ages of 10 and 30, or about 825 pounds per year. In this 20-year period the average annual litter production was probably two to three times that amount, i.e. 1614 pounds (Owen 1954) to about 2550 pounds (from Figure 3 rather than litter traps). The total calculated increment for the 20-year period is thus probably in the range of 32.3 to 51.0 thousand pounds, but the actual gain was only 16.5 thousand pounds.

The 51 to 68 percent which disappeared is thus a rough estimate of overturn rate. This rate for aspen is somewhat higher than that estimated for hardwood leaves by Maki (1951) who used metal containers

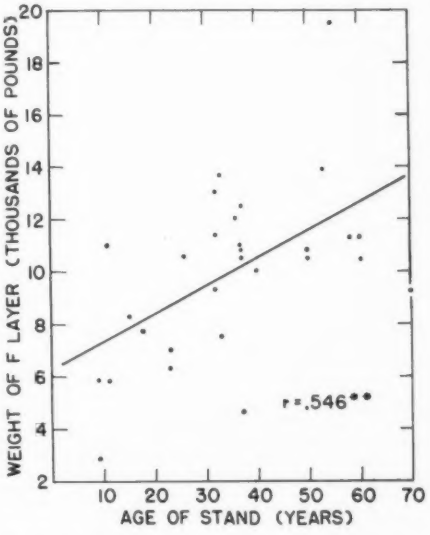


FIGURE 4. *Oven-dry weight per acre of* F *layer of 29 Minnesota plots as related to age of stand.*

wish copper-mesh bottoms with known weights of leaves which were reweighed periodically.

Nitrogen Distribution in the Profile

Nitrogen analyses of each of 5 profiles (Table 1) indicates that the F layers had substantially higher values than H layers. The A_1 layers averaged 0.327 percent, while A_2 averaged only 0.038 percent.

The calculated amounts of total nitrogen in terms of pounds per acre in these 5 profiles considering oven dry weight, depth, and bulk density were as follows: F = 188 lbs.; H = 363 lbs.; A_1 = 473 lbs.; A_2 = 294 lbs. The average oven-dry weight of the F and H layers was 11,042 and 34,032 pounds per acre respectively for these 5 plots.

Since forest fires, from the evidence at hand, often destroy all the F layer and about half the H layer, the loss of nitrogen in stands of the type discussed here would be about 370 pounds per acre. If all of it were destroyed, the amount would be 551 pounds, in the range indicated by Alway and Rost (1928).

The loss of a substantial amount of organic matter and nitrogen in forest fires and reduction of water-retaining capacity is considered a prime factor in setting back plant succession of the economically valuable climax species, such as balsam fir in Minnesota, and sugar maple and balsam fir in northern Wisconsin and Michigan. These species have rather high nutrient requirements.

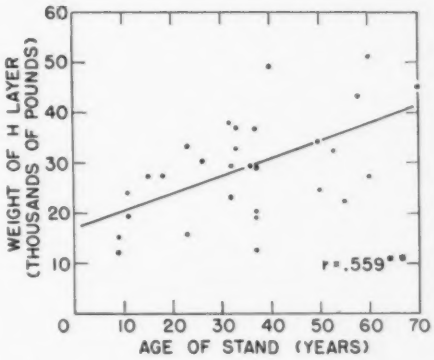


FIGURE 5. *Oven-dry weight per acre of* H *layer of 29 Minnesota plots as related to age of stand.*

Quaking aspen gradually restores not only the nitrogen fraction in surface layers by its accumulation of humus, but also bases such as potash, calcium, and magnesium. These minerals are brought by the roots from greater depths, particularly the B and C horizons and through leaf fall they enrich the H layer which contains an intensive network of fine feeder roots. These re-absorb some of the nutrients to continue the cycle.

There are large differences in the quan-

TABLE 1. Nitrogen distribution in five Minnesota soil profiles.

Plot No.	Site index	Soil type[1]	Per cent of total nitrogen in each horizon								
			F	H	A_1	A_2	B_1	B_2	B_3	C_1	C_2
1	58	Nebish l.f.s.	1.520	.580	.210	.024	.018	.023	.....	.021	.018
4	62	Nebish l.f.s.	1.650	1.200	.....	.025	.015	.025	.027	.028	.024
8	66	Dora Lake f.s.l.	1.790	.840	.280	.047	.039	.031	.009	.043	.022
11	66	Beltrami si.l.	1.710	1.220	.390	.055	.042	.056	.055	.029	.021
14	66	Nebish loam	1.840	1.470	.430	.041	.059	.046	.....	.026	.024
Average			1.702	1.062	.327	.038	.035	.036	.030	.029	.022
Ratio to C_2			78	48	15	2	2	2	1	1	1

[1]Abbreviations are as follows: l.f.s. = loamy fine sand; f.s.l. = fine sandy loam; si.l. = silt loam. Recent changes in soil series nomenclature are such that the two Nebish loamy fine sand profiles would probably be mapped as Kinghurst.

TABLE 2. Comparison of pH and of nutrients in several horizons of 21 Minnesota soil profiles, some with lime-rich parent materials and others with acid parent materials.[1]

Parent material	Horizon	pH	Total N (percent)	Avail. P (ppm)	Repl. K (ppm)	Repl. Ca (ppm)	Repl. Mg (ppm)
Lime-rich	H	5.38	1.14	170.0	86.0	779.0	81.0
	A_2	5.35	.036	27.0	7.1	39.6	5.2
	B_2	5.43	.040	34.0	17.4	190.8	39.0
Acid	H	4.97	0.96	147.0	94.0	521.0	64.0
	A_2	4.82	.060	29.0	9.3	33.3	4.4
	B_2	5.06	.025	32.0	9.8	43.9	7.3
All plots combined (weighted average)	H	5.22	1.06	161.0	89.0	680.0	75.0
	A_2	5.13	.046	28.0	8.0	37.2	4.9
	B_2	5.28	.034	31.0	14.5	134.8	26.9
Ratios for combined plots[2]	H	1.1	23.1	5.8	11.2	18.3	15.3
	A_2	1.0	1.0	1.0	1.0	1.0	1.0
	B_2	1.1	0.74	1.1	1.8	3.6	5.5

[1]The average site index for 13 lime-rich and 8 lime-poor areas was 72 and 62 respectively or a weighted average of 68 for all 21 plots. The mean annual increment was 65 and 58 cubic feet per acre for lime-rich and lime-poor plots respectively. The nutrient symbols P, K, Ca, and Mg refer to phosphorous, potash, calcium, and magnesium respectively.

[2]Using values for the A_2 as unity, i.e. 1.0 for a basis of comparison.

tities of nutrients in the various horizons. The ratios of the values for nutrients in H layer to the A_2 layer is especially striking (Table 2). In comparing lime-rich with lime-poor profiles (based on effervescence of the C_2 horizon with dilute hydrocholoric acid) there was a considerable contrast in calcium and magnesium content for the H and A_2 layers and a very marked difference in the B_2 layers.[1] Calcium was 4.4 times more abundant, and magnesium 5.4 times more abundant in the B_2 horizon of the profiles where the parent material showed effervescence with the acid. The latter are in the gray-wooded classification of forest soils.

[1]This procedure was adopted as a simple field method of separating profiles rich in lime carbonate from those without free carbonates. It does not imply that all acid soils are necessarily poor in lime, but the general validity of the method has long been accepted by soil classifiers and mappers as a primary means of separating broad genetic groups of soils.

Summary

In stands of quaking aspen in northern Minnesota the litter per acre varied from about 3200 pounds of oven-dry material in 33-year-old stands to slightly over half that amount in 10-year-old stands.

The combined weight of the F and H layers varied from 17 thousand to 62 thousand pounds per acre and was related to age of stand.

The H layer constituted as much as 70 to 90 percent of the weight of the entire organic layer. It is deduced that the forest fires which established the aspen stands did not destroy all of the organic layer of the previous stand but left a residue of around 17 thousand to 20 thousand pounds of organic material per acre, or about half the weight of the combined F and H layers found in the sample aspen stands at age 40.

The net annual increment in weight of organic layers between ages 10 and 30 for 29 plots was about 825 pounds per acre. It was calculated that from one-half to two-thirds of the organic matter produced was

lost by incorporation into the soil or disappeared due to action of organisms, and leaching.

The calculated average amount of nitrogen in the organic layers of 5 well established aspen stands was 188 pounds per acre in the F layer, and 363 pounds per acre in the H layer. It was estimated that repeat burns in stands of the type discussed, often consume about 370 pounds of nitrogen per acre, thus causing a setback in the ecological succession of the economically valuable climax species having rather high nutrient requirements.

Quaking aspen gradually restores the nitrogen in the surface layers of burned-over sites by deposition of leaf litter as well as restoring bases such as potash, calcium and magnesium brought up by root action from lower levels.

The H layers in aspen stands growing on soils with an abundance of lime carbonate had a considerably higher content of available calcium and magnesium than those on the more acid soils. The former had a site index of 10 feet more or 16 percent greater, and a mean annual increment of 7 cubic feet or 12 percent more, per acre, than the more acid soils.

Literature Cited

ALWAY, F. J. and C. O. ROST. 1928. Effect of forest fires upon the composition and productivity of the soil. Proc. First Intern. Congr. Soil Sci. 3:546-576.

ASSOC. OFFIC. AGR. CHEM. 1950. Official methods of analysis. Assoc. Official Agricultural Chemists, Washington, D. C.

CHAPMAN, H. D. and W. P. KELLEY. 1930. The determination of the replaceable bases and the base-exchange capacity of the soil. Soil Sci. 30:391-406.

CHASE, C. D. 1947. Aspen availability and supply. Lake States Forest Exp. Sta., For. Ser., U. S. Dept. Agric. Aspen Report No. 2, 15 pp.

DAUBENMIRE, R. 1953. Nutrient content of leaf litter of trees in the northern Rocky Mountains. Ecology 16:640-647.

GEVORKIANTZ, S. R. and L. P. OLSEN. 1955. Composite volume tables for timber and their application in the Lake States. U. S. Dept. Agric. Tech. Bul. 1104, 51 pp. illus.

HOOVER, M. D., and H. A. LUNT. 1952. A key to the classification of forest humus types. Soil. Sci. Soc. Amer. Proc. 16:368-370.

HORN, ARTHUR G. 1950. Commodity drain from forests of the Lake States. Lake States Forest Exp. Sta., For. Ser., U. S. Dept. Agric. Misc. Report No. 18.

KITTRIDGE, JOSEPH JR., and S. R. GEVORKIANTZ. 1929. Forest possibilities of aspen lands in the Lake States. Univ. of Minn. Tech. Bul. 60, 84 pp., illus.

MAKI, T. EWALD. 1951. Some factors affecting the composition and development of forest floor. Ph.D. Thesis, Univ. of Minn. Soils Dept. 85 pp.

OWEN, T. H. 1954. Observations on the monthly litter-fall and nutrient content of Sitka spruce litter. Forestry 27 (1): 7-15.

ROWE, J. S. 1953. Forest sites—a discussion. For. Chron. 29:278-289.

SNEDECOR, GEORGE W. 1937. Statistical methods. Collegiate Press Inc., Ames, Iowa, 341 pp., illus.

STOECKELER, JOSEPH H. 1960. Soil factors affecting the growth of quaking aspen forests in the Lake States. Univ. of Minn. Tech. Bul. 233, 48 pp., illus.

TRUOG, E. 1930. The determination of the readily available phosphorous of soils. J. Am. Soc. Agron. 22:874-882.

Equations for the Description of Past Growth in Even-Aged Stands Of Ponderosa Pine

BY
CHARLES F. COOPER

OVER THE YEARS many mathematical models have been proposed to describe biological growth processes. Some of these have been developed by foresters; others, originated by workers in other fields, have been applied to forest trees. There is still no agreement on the one best expression for the description of growth phenomena.

A group of Japanese investigators, studying growth and intraspecific competition in herbaceous plant communities, have proposed several equations to describe the relationship between mean plant weight and stand density at various ages. These equations give a satisfactory fit to data derived from several even-aged stands of ponderosa pine (*Pinus ponderosa* Laws.) in northern Arizona, and appear to offer promise as a means of analyzing some aspects of growth in forest stands.

Collection of Data

Field work for this study was carried out in the fall of 1957 at two locations on the Fort Apache Indian Reservation in east central Arizona (1) near Bog Creek, about 10 miles east of the town of McNary and (2) on Odart Mountain, some 7 miles west of Maverick. These two points are about 40 miles apart, but are closely similar in elevation, topography, and soils. Both are in the heart of some of the best and most productive pine forest in Arizona.

Sampling was limited to pure stands of even-aged ponderosa pine of pole size. In the dry climate of the Southwest, only in occasional years are favorable weather and a good seed crop so synchronized as to permit establishment of abundant reproduction. In a single stand of sapling or pole size, every tree almost without exception will have begun its growth in the same year, so that age differences among trees can be ignored.

Selected stands at each location were sampled, using 1/10-acre, 1/40-acre, and 1/100-acre circular plots placed to include as many as possible of the typical conditions of stand age and stocking density in the area. Plot size was chosen to include approximately 30 to 50 trees on each. On every plot, diameter at breast height of each tree was measured; and on most, all trees less than about 5 inches d.b.h. were felled and a circular cross section taken from each. Increment cores, at about 9 inches above the ground, were taken from the few trees that remained uncut. On 4 plots only a random sample, comprising about one-fourth of all the trees, was cut

---

The author is now with the Watershed Technology Research Branch, Agricultural Research Service, U. S. Department of Agriculture, Boise, Idaho. Manuscript received Aug. 12, 1959.

Field work for the study was supported in part by the National Science Foundation through the Botany Department at Duke University. Thanks are due to the Tribal Council, White Mountain Apache Tribe, for permission to carry out the field work on their tribal lands and to Orval Klose, professor of mathematics, Humboldt State College, for advice and criticism.

or bored. Of the 14 stands included in this analysis, 3 originated in 1903, 7 in 1909, and 4 in 1914. Size of individual trees on the plots ranged from less than 0.5 inch to about 11 inches d.b.h. Stand density varied from the equivalent of 360 to 8500 stems per acre.

The cores and stump sections were surfaced, and ring counts made to determine the diameter inside bark of each tree at several earlier periods. Because of the need to determine tree ages precisely for this and other concurrent studies, sections were taken as close to the ground as possible. Unless otherwise stated, all diameters refer to measurements inside bark at or near ground level. A regression equation based on 94 trees over 4 inches d.b.h. indicated that diameter inside bark near ground level is equal to 0.93 d.b.h. The standard deviation of this regression coefficient is 0.014.

Cross-sectional stem areas in square feet per acre were computed from the diameter data for each stand. The term "stem area" will be used to denote the cross-sectional area derived from diameter measurements at ground level. Stem areas were computed at the time of harvest and at each earlier ten-year interval in the life of the stand. Additional interpolated measurements of the 1909 stands made possible the comparison of stem areas of all stands at a common age.

Most studies of growth in forest stands have dealt only with trees of merchantable size, or with potential crop trees. Analysis of total production of plant material, however, requires inclusion of every tree, including those that will not contribute to final harvest. Total stem area per acre for each stand was divided by number of trees to find the average cross-sectional area. The latter was used as the primary dependent variable in fitting the data to equations previously used for herbaceous plants.

The past stem areas calculated here obviously include only those trees that were present in the stand in 1957; the areas for previous years include no allowance for trees that have since died. For the present analysis, however, this is of no importance, since this study is concerned with the past growth of those trees that make up the present stand. Natural mortality in these ponderosa pine stands is exceedingly low in the absence of fire, and is concentrated almost wholly in the smallest size classes (Cooper 1960).

Relations of Stem Area to Age and Stand Density

Kira *et al.* (1953) planted soybeans at five different grades of stand density, and measured the total weight per plant at six separate times during the 119-day growing season. They found that the relationship of mean plant weight to density at any given time could be represented by

$$w\rho^a = K \qquad (1)$$

where w is mean weight per plant, ρ is stand density, and a and K are constants. They showed that this equation is applicable to a wide range of data, their own and that of other researchers.

They found that the exponent a increased from zero at time of germination to approximately 1 at time of equilibrium, when dry weight per plant was inversely proportional to stand density. The value of a, from germination to equilibrium, increased as a linear function of the logarithm of time. Kira *et al.* considered that the exponent a represented the degree of space utilization by an individual plant at a given stage of growth. They named this exponent the *C-D* (Competition-Density) *Index*, and termed the relationship symbolized in (1) the *C-D Effect*. The C-D relationship assumes that final yield per acre at maturity is a constant regardless of plant density, an assumption generally supported by studies of pasture plants and by forest yield studies.

The soybean experiments dealt with plants distributed uniformly on the plots. Further investigations (Kira *et al.* 1956) showed experimentally that the C-D effect holds equally well for plants non-uniformly distributed. The C-D relationship likewise

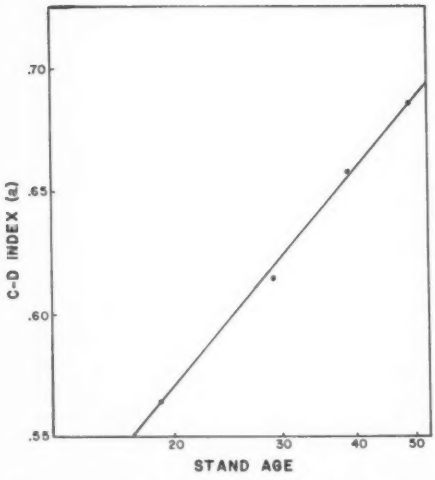


FIGURE 1. *Variation with time of the Competition-Density Index, the exponent in the C-D equation (1).*

proved applicable to natural communities of weeds and to young stands of Japanese red pine (*Pinus densiflora*). In the same paper it was demonstrated that the identical form of equation holds regardless of whether plant weight or some indirect measure such as basal area is used in the calculation, and regardless of whether mean plant weight is based on initial plant

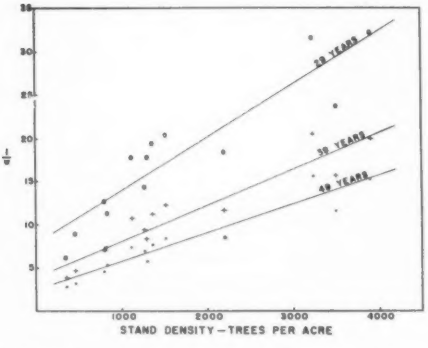


FIGURE 2. *The relationship between the reciprocal of mean stem area per tree and stand density at different ages.*

density or on plant density at time of sampling. Of course, if natural mortality has reduced stand density in the time since planting, the numerical values of a and K in (1) will depend upon whether initial or present density is used to compute mean plant weight. Evidently, then, there is no barrier to the application of equation (1) to the 14 pine stands, where the individual trees in each stand are distributed irregularly, and the only density data available are those at time of final sampling.

In order to fit observed data to the C-D equation, the latter can be expressed in the form

$$\log w = \log K - a \log \rho \qquad (2)$$

Mean stem area per tree plotted against stand density should give a straight line on log-log paper if the above equation holds; likewise, the fit of equation (2) can be tested by regression. Separate regressions of stem area on stand density, in the form of (2), were calculated for the 14 pine stands at each of 4 ages. Interpolated measurements were used where necessary so that all the mean stem areas used in any equation were based on the same stand age.

In all 4 equations, the regression coefficients were significant at the 1 percent level. Furthermore, as predicted by the C-D theory, the four calculated values of a fell on a straight line when plotted over the logarithm of time (Fig. 1), indicating an increasingly efficient utilization of space with the progress of time.

Upon further analysis, the same group of Japanese investigators who first proposed the C-D equation suggested another form of the relation between mean plant weight and stand density (Shinozaki and Kira 1956). They pointed out that data on mean weight (or stem area) and stand density at any given time can be fitted to the equation

$$1/w = A\rho + B \qquad (3)$$

where A and B are parameters whose values change with time, and w and ρ are the same as before.

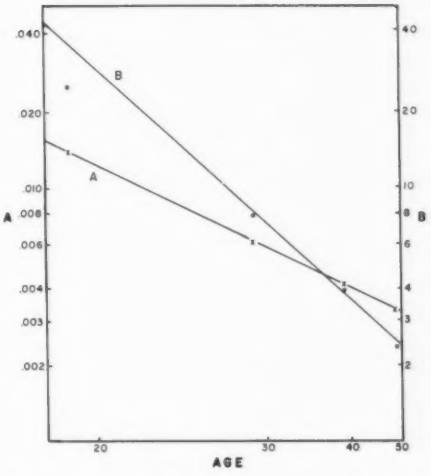


FIGURE 3. *Variation with time of the coefficients* A *and* B *in the reciprocal equation (3).*

Four separate regression equations were calculated relating mean stem area per tree at four ages in the past to present stand density of the 14 pine stands. This time, (3) was used as the form of the regression (Fig. 2). Once again, the regression coefficients were significant at the 1 percent level. When plotted against the reciprocal of time, the logarithms of both A and B fell very nearly on straight lines (Fig. 3).

The Logistic Growth Equation

In their study of several different growth curves, Shinozaki and Kira (1956) showed that field data conforming to the reciprocal equation (3) can be fitted to the well-known logistic equation. Before attempting to do so, it is necessary to consider some of the properties of the logistic equation, and the assumptions underlying its derivation.

The rate of increase, in absolute numbers, of any population growing in unlimited space may be expressed as

$$\frac{dN}{dt} = r_m N \qquad (4)$$

where N is the size of the population at time t, and r_m is a parameter that may best be designated the *intrinsic rate of natural increase*. The rate of increase of the same population growing in limited space is

$$\frac{dN}{dt} = (r_m - cN)\,N\,. \qquad (5)$$

Here N is the density of the population, or number per unit area, while c is the constant amount by which the intrinsic rate of natural increase is reduced by the addition of one more individual to the population already present in unit space. The instantaneous relative rate of increase, or rate of increase per unit of population, is found by dividing both sides of the equation by N, so that

$$\frac{1}{N}\frac{dN}{dt} = r_m - cN\,. \qquad (6)$$

Equation (6) is the differential form of the logistic equation (Andrewartha and Birch 1954).

In the last 30 years the logistic equation has been used to describe a variety of growth phenomena, and much has been written about its applicability. The logistic theory of growth presupposes that every species has a definite intrinsic rate of natural increase which is a constant in a given environment and which is as characteristic of the species as any other taxonomic or morphological feature (Andrewartha and Birch 1954). For any given species, therefore, r_m is considered to have a definite value which is dependent upon the particular set of environmental conditions currently operative. It is, in short, a theoretical exponential rate at which a population might be expected to increase in a given environment if unimpeded by the influence of other organisms of the same kind. Andrewartha and Birch (1954) have presented data from studies of insects and other animal populations to support the conclusion that there exists an attribute of animals corresponding to the intrinsic rate

of natural increase.

The logistic equation is more familiar in its integrated form:

$$N = \frac{K}{1 + e^{k - r_m t}} \qquad (7)$$

Here k is the constant of integration, the constant K is the asymptotic value toward which N tends as time t approaches infinity, and e is the base of natural logarithms. A biological interpretation of K suggests that it is the density at which the particular space under consideration becomes "saturated" with the organisms involved.

The simple logistic equation has been successfully fitted to the growth of animal populations. It apparently does not adequately describe the growth of plant communities, although MacKinney *et al.* (1937) successfully applied it to loblolly pine stands. A basic assumption of the logistic theory is that r_m remains constant with time. Shinozaki and Kira (1956) have suggested that the intrinsic rate of natural increase may actually change as plants grow older, so that $r_m = f(t)$. The simple logistic equation (7) can then be modified by substituting

$$\int_0^t f(T)\, dT \qquad (8)$$

for $r_m t$. This integral is essentially equivalent to the sum of all the infinitesimally changing values of r_m from time zero to the time at which the value of the integral is desired. Shinozaki and Kira refer to the modified equation as a generalized logistic equation.

Fitting Field Data to the Logistic Equation

Shinozaki and Kira (1956) used a complicated graphical method to relate their data to the logistic equation. A simpler method is based on the well-known fact that the instantaneous relative rate of increase r in any population can be estimated by

$$\frac{1}{N}\frac{dN}{dt} = r = \frac{\ln N_2 - \ln N_1}{t} \qquad (9)$$

where N_1 and N_2 are the sizes of the population at any two known times and t is the time interval between measurements. It is evident that the shorter the time interval t, the better is the estimate of r, provided that there are no great year to year variations in growth due to varying environments.

The instantaneous relative rate of increase in stem area was calculated for the 14 pine stands from equation (9), using mean stem area per tree as the estimate of population size. An estimated value of r was calculated for 3 ten-year periods in the life of each stand: 1928-1937, 1938-1947, and 1948-1957. The rate of increase so calculated is actually the integral of all the changing rates that prevailed over a ten-year span. The year-to-year variations in growth that became more noticeable as the period between measurements is shortened precluded the use of a shorter interval than 10 years in the calculation of r.

It was apparent that the calculated instantaneous relative rate of growth declined from decade to decade. According to the simple logistic theory, the only factor that should have contributed to the decrease in observed growth rate was the continual increase in tree biomass present per unit area. Plotting of the data indicated, however, that this was not a sufficient explanation. There was also a nearly linear relation between instantaneous growth rate r and the reciprocal of stand age. This suggests that the intrinsic rate of natural increase, r_m, in these stands is not a constant but may be made up of a component independent of time and a component that varies as the reciprocal of time, so that

$$r_m = r_0 + r_1 \frac{1}{t}. \qquad (10)$$

According to the logistic theory, the intrinsic rate of natural increase is lowered an amount c by the addition of each new increment to the population. The proper

measure of this increment is obvious in the case of animal populations — it is clearly just the number of animals added to unit space. In the plant community, though, the number of organisms is less important in its influence on growth rate than is some other measure of population size such as weight or volume of vegetation.

The measure of space occupancy most commonly used by foresters is basal area, which is closely related to the stem area at ground level used in this study. Plotting the instantaneous relative rate of growth, r, against stem area per acre yields a curvilinear relationship whose points show considerable scatter. This line can be rectified by assuming that the parameter c varies inversely with time.

A simpler hypothesis gives a better fit to the data, however. Rate of growth bears a linear relation to population size if the sum of all tree diameters per acre is used instead of stem area or basal area. This is logical when it is considered that stem diameter is almost directly proportional to the surface area of the cambium, whereas stem cross-sectional area is related to cambial area by a square root function. Lexen (1943) has suggested that total bole surface per acre is a better measure of stocking in forest stands than is basal area, since the bole area is actually the base upon which new growth is laid down.

Significant quantities of carbohydrates that might otherwise be stored as new wood are utilized by the cambium in respiration. The extent of this respiration is dependent upon the total surface area of cambium present. In stands of comparable height, one composed of many small trees will have a greater area of respiring cambial surface per acre than will one with the same basal area concentrated in a few large trees. The stand with the higher total rate of respiration might be expected to exhibit a slower growth rate. The direct relationship between stem diameter and surface area of cambium makes it appear that the sum of tree diameters per acre is a better measure of the influence of stand density in impeding growth rate than is basal area. This conclusion was confirmed in the present study.

Substituting (10) in the differential form (6) of the logistic equation,

$$r = r_o + r_1 \frac{1}{t} - cS \qquad (11)$$

where S is the sum of all tree diameters per acre and t is stand age. This equation can be solved by least squares, and its applicability to the data at hand tested. Since the calculated values of r used in this solution are estimates of the mean instantaneous relative rate of stem growth over a ten-year period, the value of S should be an average of the diameter sums at the beginning and the end of each decade. Mathematical considerations dictate the choice of the geometric mean of S_1 and S_2, or $\sqrt{S_1 S_2}$, as the proper estimate of S to insert in equation (11). The correct value of t is the age midway between the time of measurement of consecutive values of S.

Based on data from the 14 pine stands,

$$r = 2.91 \frac{1}{t} - 0.0000359\, S\,. \qquad (12)$$

Both regression coefficients were significant at the 1 percent level; the constant term r_o was not significantly different from zero. The calculated regression accounted for about 83 percent of the variance in r around its mean value.

Attempts were made to fit the data to several other equations, using total stem area per acre instead of the sum of tree diameters, and using the logarithm of time instead of its reciprocal. The expression proposed in equation (11) gave the best fit and the smallest error variance. A still better fit could probably have been obtained if, instead of the sum of tree diameters, actual bole area per acre had been used as one of the independent variables.

The intrinsic rate of natural increase, assumed in the simple logistic theory to be a constant, is shown to vary inversely with time, as suggested by Shinozaki and Kira

(1956). Equation (12) states that the instantaneous relative rate of stem growth, or rate of growth per square foot of stem area present, is inversely proportional to stand age, and that it decreases as the sum of tree diameters per acre increases.

Substituting general variables for the specific coefficients found by regression, equation (12) can be rewritten in differential form:

$$\frac{dw}{dt} = \left(\frac{r_1}{t} - cS\right) w \qquad (13)$$

where, as before, w is mean stem area per tree, S is the sum of all tree diameters per acre, t is stand age, and r_1 and c are constants. This equation can be integrated, but the integration is laborious and the resulting expression somewhat unwieldy. The graph of the integrated form of equation (13) is a more or less bell-shaped curve, with a rising sigmoid portion which reaches a maximum value of w and then declines to zero. The rising limb of this curve adequately describes the growth of the trees in the ponderosa pine stands studied here. The data used in fitting the equation fell near the point of inflection of the sigmoid curve, making it relatively easy to fit tree areas to the assumed curve. The data could as well have been fitted to any of several other equations.

Discussion

Any acceptable growth equation must of course fit the data which it purports to describe. Mere closeness of fit to field observations is no guarantee of its validity, however. Unless the parameters of a proposed growth equation can be shown to have some biological meaning, its application is little more than an exercise in mathematical curve fitting. The coefficients of a purely empirical equation have no definite physiological basis, and there is no way of knowing how they might change with variations in stand conditions.

The existence of real attributes of animal populations corresponding to the parameters of the logistic equation has often been suggested. In insect populations, and perhaps in other animal populations as well, there is evidently an intrinsic rate of natural increase that is characteristic of the species. This theoretical rate is never realized in the field, but it can be calculated from the birth rate, death rate, and age structure of the population (Andrewartha and Birch 1954). The observed population growth rate is the intrinsic rate of natural increase reduced by an amount proportional to the number of individuals present in unit space (Equation 6).

The logistic equation adequately describes the stem area growth of the ponderosa pine stands studied here if it is assumed that the intrinsic rate of natural increase is inversely proportional to stand age rather than a constant. It is clearly possible to assign a real biological meaning to the coefficient c in equation (12). It is the amount by which the instantaneous growth rate is reduced by the addition of each new increment of respiring tree surface to the stand.

A rational interpretation of the intrinsic rate of natural increase itself is less easy, for unless some logical reason can be shown for the variation of this rate with time, it becomes merely a means of fitting an empirical equation to observed data. A possible explanation lies in the fact that as a tree grows older and increases in size, it requires a greater quantity of soil nutrients. The root system can effectively expand in only two dimensions while the aboveground portion is growing in three, and even lateral expansion is restricted by the roots of other trees. Thus the root system becomes progressively less able to supply all the tree's needs as the tree grows older, and the growth rate declines due to the lowered root effectiveness per unit of tree biomass.

Other Growth Equations

Beverton and Holt's (1957) comprehensive treatise on the growth and dynamics of fish populations deserves careful study by students of tree growth, for fishes and trees have much in common. Both continue

growing more or less throughout their lives, and the growth of both is remarkably responsive to environmental influences.

Beverton and Holt (1957:97) reviewed many of the published growth equations, and concluded that most were unsuitable for description of the growth of fishes. Either their constants had no biological meaning, the equations were based on faulty physiological assumptions, or they did not adequately fit the observed pattern of growth. The latter criticism was directed against the simple logistic equation, which gives a symmetrical s-shaped curve that does not correspond to the actual growth of either trees or fishes. The point of inflection in both classes of organisms comes relatively early in life. Pearl and Reed (1923) introduced the necessary asymmetry into the simple logistic equation by adding a polynomial in t, but this modification is wholly empirical, with less biological meaning than equation (13).

The equation that Beverton and Holt found most appropriate to the growth of fishes was that of von Bertalanffy (1938). This is of the same general mathematical form as the logistic, but Beverton and Holt considered that its coefficients conformed more closely to the physiological characteristics of fish growth. Their exhaustive treatment of population dynamics is largely built around this equation. It may be equally applicable to the growth of trees.

The von Bertalanffy equation requires more data for its satisfactory fitting than were available here. A graphical method for the handling of this equation was given by Beverton and Holt (1957:282). Preliminary plotting of the data from the 14 pine stands indicates that the Bertalanffy equation may give a good fit. More recently, Parker and Larkin (1959) have criticized certain features of the Bertalanffy equation as it applies to the growth of fishes. Their criticisms appear to be equally pertinent to the problems of tree growth. They have suggested a parabolic equation which, together with some of the methods of Beverton and Holt, may prove highly suitable for analysis of the growth of trees.

Summary

Two equations relating mean basal area per tree to stand density have been found applicable to even-aged stands of ponderosa pine in northern Arizona. These equations proved equally applicable to past areas obtained from ring counts. Data on mean basal area per tree at several past ages have been fitted to the well-known logistic curve. The logistic equation gives a satisfactory fit to the growth of these stands if it is assumed that the parameter commonly known as the intrinsic rate of natural increase is not a constant but varies inversely with time.

The measure of population size most closely related to the instantaneous relative rate of growth in these stands was the sum of all tree diameters per acre rather than the conventional basal area per acre. This is logical when it is considered that diameter bears a more direct relationship to the surface area of the cambium than does basal area.

Additional equations that have proved satisfatory for description of the growth of fishes are suggested for analysis of the growth of forest trees.

Literature Cited

ANDREWARTHA, H. G. and L. C. BIRCH. 1954. The distribution and abundance of animals. Chicago: Univ. Chicago Press. 782 pp.

VON BERTALANFFY, LUDWIG. 1938. A quantitative theory of organic growth. (Inquiries on growth laws, II.) Human Biol. 23:302-312.

BEVERTON, R. J. H. and S. J. HOLT. 1957. On the dynamics of exploited fish populations. Min. Agr. Fish. and Food U. K., Fisheries Invest. Ser. II, 29:1-533.

COOPER, CHARLES F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecol. Monog. 30:129-164.

KIRA, T., H. OGAWA, and N. SAKAZAKI. 1953. Intraspecific competition among higher plants. I. Competition-yield-density interrelationships in regularly dispersed populations. J. Inst. Polytech. Osaka City Univ. 4(D):1-16.

————, H. OGAWA, K. HOZUMI, H. KOYAMA, and K. YODA. 1956. Intraspecific competition among higher plants. V. Supplementary notes on the C-D effect. J. Inst. Polytech. Osaka City Univ. 7(D):1-14.

LEXEN, BERT. 1943. Bole area as an expression of growing stock. J. For. 41: 883-885.

MACKINNEY, A. L., F. X. SCHUMACHER, and L. F. CHAIKEN. 1937. Construction of yield tables for nonnormal loblolly pine stands. J. Agric. Res. 54:531-545.

PARKER, ROBERT R. and PETER A. LARKIN. 1959. A concept of growth in fishes. J. Fish. Res. Bd. Canada 16: 721-745.

PEARL, R. and L. J. REED. 1923. On the mathematical theory of population growth. Metron 3:6-19.

SHINOZAKI, K. and T. KIRA. 1956. Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. J. Inst. Polytech. Osaka City Univ. 7(D):35-72.

Commonwealth Forestry Bureau

Oxford, England

Forestry Abstracts

This presents the essence of current world literature extracted by an experienced permanent staff from publications in about 30 languages (over 550 periodicals, 750 serials and innumerable miscellaneous papers, books, etc.) and now totalling over 4,500 abstracts each year. Special features include: the abstracting at length of literature published in the more unfamiliar languages (e.g. Slav, Hungarian and Oriental languages); notices of the more important critical reviews; notices of translations into English; notices of new journals and serials, or of changes in their style; and notices of atlases, maps and patents. Each issue normally contains a leading article synthesizing authoritatively the litertaure on some particular subject and also items of world news. Annual subscription is £3.10. or $9.80 U.S.A. or Canada.

Guide to the Use of Forestry Abstracts

Containing a directory of publishing sources, analysis of an abstract notice, a key to abbreviations and many other aids, now available in an enlarged 4-language edition (English, French, German, Spanish) for 10s. or $1.40 post free.

Centralized Title Service

A quick-service postal auxiliary to the Abstracts bringing to subscribers four times a month exact copies of the index cards made from the world stream of forestry literature during the Bureau's day-to-day work, totalling about 6,500 annually. Full particulars and samples from: The Director, Commonwealth Forestry Bureau, Oxford.

Orders should be sent to:

Central Sales Branch, Commonwealth Agricultural Bureaux, Farnham Royal, Buckinghamshire, England

Effects of Photoperiod and Source on Seedling Growth of Eastern Hemlock

BY
HANS NIENSTAEDT
J. S. OLSON

MANY PROVENANCE TESTS of trees have been made in the field, but few indoors under controlled conditions of photoperiod and temperature. Seedlings of eastern hemlock, *Tsuga canadensis* (L.) Carr., have low light requirements and are therefore well suited to indoor experiments on the effects of both genetic and environmental factors. Such experiments have been carried on in Connecticut since 1952.[1] The present paper shows how genetic differences among seedlings from 30 sources of hemlock, combined with photoperiod and thermoperiod, account for relatively large differences in the duration and amount of seedling stem elongation.

Review of Literature

Racial variation. The importance of seed source for forest tree growth was first suggested by Duhamel du Monceau in France (Syrach Larsen 1949). But it is mainly in the last 50 years that the implications of genetic differences have been tested and applied by foresters. The earliest studies with native American species in North America were established by Zon with ponderosa pine, *Pinus ponderosa* Laws., in 1911 and with Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in 1912. Both tests clearly showed the importance of seed origin (Munger and Morris 1936, Weidman 1939, Munger 1947).

Since these early experiments, provenance tests have demonstrated the importance of seed origin for a number of native species. Among these are: red pine, *Pinus resinosa* Ait., by Rudolf 1947, Hough 1952a, b; jack pine, *P. banksiana* Lamb., by Schantz-Hansen and Jensen 1952; loblolly pine, *P. taeda* L., by Wakeley 1944, 1954; lodgepole pine, *P. contorta* Dougl., Critchfield 1957; white spruce, *Picea glauca* (Moench) Voss, by Rudolf 1953; and sugar maple, *Acer saccharum* Marsh., by Kriebel 1957. All show very striking effects of seed origin, but, except for the work by Critchfield and Kriebel, they give little information regarding the relative plasticity of the different species and practically none regarding the delineation of races within the species.

Recently large-scale studies have been established. They include in the southern states the four important pines: slash, *Pinus elliottii* Engelm.; loblolly; shortleaf, *P. echinata* Mill.; and longleaf, *P. palustris* Mill.; and in the Lake States region, jack pine and white spruce. Other species under investigation are red pine, white pine, *Pinus strobus* L., northern red oak, *Quercus*

[1]Background and results of this and other research, and acknowledgments of aid from many individuals, have been brought together in Bulletin 620 of the Connecticut Agricultural Experiment Station, New Haven, 1959.

The senior author is Geneticist, in charge Northern Institute of Forest Genetics, a field unit of the Lake States Forest Experiment Station, Forest Service, U.S. Department of Agriculture. The junior author, while working on this study, was Associate Forest Ecologist at the Connecticut Agricultural Experiment Station; he is now Geobotanist at the Oak Ridge National Laboratory, Oak Ridge, Tenn. Manuscript received Dec. 21, 1959.

rubra L., various species in the genus *Populus*, and the more important western conifers.

Field testing will always be a part of seed source studies, and the ultimate selection of desirable sources must be based on field tests. Certain types of racial variation may, however, be studied at the seedling or even cotyledon stage by growing the plants under artificially controlled conditions (Schmidt 1951). Kramer (1936) noted that knowledge of the optimal photoperiod should aid in predicting whether or not a given species is suitable for growth at any given latitude. His statement may be extended to include different races within the same species.

Photoperiod and growth responses in forest trees.—Photoperiod—the durations of the daily exposure to light and dark—has a marked effect on the cessation of growth, leaf fall, and to some extent on the breaking of dormancy (Wareing 1948, 1956). Different species may react very differently to a given daylength. Moshkov and Bogdanov, working independently of each other, studied the photoperiod responses of several species from 17 different tree genera (Gevorkiantz and Roe 1935). A shortening of daylength resulted in a decrease in the length of growing period, that is, premature cessation of growth and more rapid hardening of the young shoot. Some of the southern species, if grown on natural daylength (Leningrad, maximum 20 hours), continued growing into the fall and suffered severe frost injury. If grown on short daylength, they would ripen early and survive the winter without injury.

Kramer (1936) studied 10 native North American species, including one conifer. On short-day treatments (8½ hours) all species except one grew less and became dormant sooner than the plants on normal daylength. When exposed to long days the responses differed among species—ranging from continued growth throughout the winter to little or no effect of increased daylength. Long-day treatments also resulted in earlier breaking of dormancy than did short-day treatments. A light intensity of 2 foot-candles, or even less, was sufficient to bring about the type of responses observed (Kramer 1937).

The variation between species in response to different photoperiod depends on the time at which growth stops in nature (Downs and Borthwick 1956). Horsechestnut, *Aesculus hippocastanum* L., which stops growth in June and July, was the least sensitive to long days; elm, *Ulmus americana* L., which grows until frost, was the least sensitive to short days. However, long days will result in some extension, short days in a shortening of the period of elongation.

Photoperiod and racial variation in forest trees. Photoperiod responses of trees of different provenances of the same species often follow a definite clinal variation pattern (Langlet 1942-1943, Sylven 1940). At a given latitude local types of aspen and Scotch pine, *Pinus sylvestris* L., have their annual growth rhythm adjusted to the prevailing daylength regime. If trees are moved northward, the growth period lengthens, with corresponding late shoot ripening and possible injury from fall freezes. Provenances moved southward will cease growing early in the season even though other climatic factors are favorable for growth.

Pauley and Perry (1954) have reported similar results from a study of black cottonwood, *Populus trichocarpa* Torr. & Gray, and eastern cottonwood, *P. deltoides* Bartr., and showed that the variation in the date for cessation of height growth is definitely clinal in nature, although a local diversity of photoperiodic responses occurs among clones independently of latitude of origin. They advanced the hypothesis that adaptation to any particular length of growing season results from the natural selection of the genotypes which have a suitable response to the prevailing daylength regime of the latitude.

Preliminary results with Douglas-fir by

Irgens-Moller (1957) suggest that high-altitude genotypes may be more sensitive to photoperiod than low-altitude types because of the greater survival value of the individuals that are well adapted to the more rigorous climate.

Thermoperiodism in trees. Kramer's (1957) review indicates that surprisingly little attention has been paid to temperature responses, particularly the so-called "thermoperiodic" responses, i.e., responses resulting from differences in day and night temperature. His results with loblolly pine and the following results with hemlock suggest that diurnal temperature changes and photoperiod may both have important effects on seasonal growth and geographic distribution, and that adaptations to both these factors differ within widespread forest tree species.

Photoperiodic and thermoperiodic responses in hemlock. Preliminary experiments with 2-year-old seedlings from a Connecticut source (Olson and Nienstaedt 1953, 1957) showed striking differences in growth under 8, 12, 16, 20, and 24 hours of illumination. As in Scotch pine (Wareing 1950), a combination of 20-hour days and 4-hour nights showed the best growth. Interruptions of the dark period by dim light also confirmed Wareing's demonstration that tree growth, like many other photoperiodic responses, seems more affected by duration of the dark period than of the light period; hence photoperiodic effects will be described in this paper by nightlength. The favorable effects of high day-low night temperature combinations were also indicated in 10 combinations of day and night temperature.

The present study, with a more closely spaced series of nightlength treatments between 8 and 12 hours and a wider range of temperature combinations, has confirmed these relations. It incorporated 30 seed sources and consistently showed differences between seed sources that appear to represent genotypic variation resulting from adaptation to local climatic conditions.

Materials and Methods

Sources of material. Eastern hemlock covers roughly a triangular area in eastern North America from Nova Scotia and Quebec (lat. 48° N.) to Minnesota and south to northern Alabama (34°30′ N.). In the north it grows from sea level to an elevation of perhaps 1,600 to 1,800 feet and in the south from about 1,000 to about 4,800 feet, with an occasional outlier at 700 to 800 feet and at least one as low as 500 feet.

In 1953 seed was collected from 30 locations. They spanned most of the latitudinal, longitudinal, and altitudinal range of hemlock. Several sources were from different altitudes in the same general latitude. Figure 1 shows the location and Table 1 gives pertinent data on each seed source. In the table the sources have been arranged in four groups according to the average length of the frost-free season, based on data from a nearby official weather station adjusted to allow for differences in elevation, etc. This adjustment is only a rough one, but errors due to microclimate or lack of nearby data are probably small relative to the whole span of growing season over hemlock's range—from about 100 to 200 days.

Collections were represented by equal amounts of seed from 4 to 10 trees, except for two single tree collections (Nos. 15 and 18) near the limit of the range of the species.

After extraction the seed was cleaned and empty seeds removed in an airstream. Samples of 100 seeds were weighed (Table 1) and tested for viability by germination.

Treatments. After about 90 days of stratification at 5° C, the seed was planted in pots. Germination was generally high and pots were thinned at random to secure a good spacing of 10 to 20 seedlings in each pot.

When all the seedlings had reached the cotyledon stage and just begun to show the first new leaves (44 days after planting) they were moved to rooms or boxes where

FIGURE 1. *The geographic range of eastern hemlock, showing source numbers of seed collections used in indoor seedling experiments, and geographic trends in elongation averaged over several nightlength treatments.*

light and temperature could be controlled according to conditions given below. Plants were fairly uniform at this time although some from the more northern sources, which had partially germinated during stratification, were slightly more advanced.

All the seven photoperiodic treatments were carried out in one room, partitioned into compartments. Each compartment was furnished with banks of fluorescent daylight tubes. Light intensity was maintained at approximately 450 foot-candles (4850 lux) at plant level.

The plants were all exposed to 12 hours of the high-intensity light. To provide 12, 11, 10, 9, 8, 6, and 4 hours of total darkness in each 24 hours, additional light was furnished from 15-watt incandescent bulbs, giving from 4 to 8 foot-candles (about 40 to 80 lux) at plant level. The additional light was given following the full intensity illumination except in the 6-hour treatment where 6 hours of dim light preceded the 12 hours of full illumination. All these photoperiodic treatments were carried out at a temperature of 17° C (±2° C).

In addition another series on 16 hours of light and 8 hours of darkness was maintained at constant temperatures: 7, 17, 22, 27, 32, and 37 degrees C. By moving some plants between the different temperature conditions, a third series of alternating (day and night) temperature combinations was obtained (Table 5). These plants were exposed to high temperature approximately 8 hours and to low temperatures for 16 hours. The "day-temperature" treatment was during the period of high-intensity illumination. All seed sources were included in the daylength and constant-temperature series, but only 15 in the alternating-temperature series. All sources on all treatments were replicated as two randomized blocks.

Collection of data. The numbers of actively growing and the numbers of plants

showing buds were determined after the plants had been under treatment for 18, 33, and 88 days days or a total of 62, 77, and 132 days after sowing the seed. At the same time the number of plants showing a second flush of shoot elongation was noted; a fully matured bud stage had usually not been reached by the time this second elongation was resumed. In order to eliminate errors in measurements due to changing the soil line and to minimize seed weight effects, only elongation above the cotyledons were measured. Records were taken at intervals during the growth period of the plants, but only the total elongation at the end of the experiments is presented here. The heights were recorded to the nearest millimeter.

Results

Duration of growth. Within 62 days after planting, some seedlings were already forming terminal buds under 11- or 12-hour nightlengths (Table 1). Many more formed buds in the next 15 days, under all

TABLE 1. Source of seed and photoperiod as related to period of growth of hemlock under controlled conditions.

Seed source no.	North latitude (degrees)	Altitude (feet)	Monthly mean temp. °F Jan.	Monthly mean temp. °F July	x Length of frost-free season	y Weight of 100 seed, grams	Days after planting								
							62[1]		77						
							Nightlength in hours								
							12	11	12	11	10	9	8	6[2]	4
							Percentage of plants growing								
15[3]	35°45′	1,000	40	77	195	.342	100	100	0	20	5	39	45	0	100
7	41°15′	20	30	73	195	.357	100	100	0	0	20	4	91	22	67
13	35°40′	1,300	40	76	192	.357	100	100	4	50	52	55	96	92	97
17	35°40′	1,200	41	75	188	.396	100	100	0	4	7	30	76	59	100
33	42°00′	600	26	72	184	.302	100	100	0	0	0	4	56	56	92
12	35°40′	2,300	38	74	184	.374	100	100	0	54	55	48	100	73	90
10	40°18′	100	33	75	181	.386	100	100	0	33	42	71	100	52	58
20	38°15′	1,900	32	69	164	.341	100	100	0	0	0	0	71	56	28
26	42°25′	950	25	71	158	.346	100	100	0	4	7	17	71	33	81
18[3]	35°45′	4,800	34	68	156	.311	96	96	0	0	0	18	83	39	92
32	40°45′	1,000	30	74	153	.286	100	100	0	0	0	0	29	0	47
22	44°40′	100	24	65	150	.243	100	100	0	0	0	0	26	31	24
8	41°45′	500	26	70	150	.377	94	97	0	12	0	0	35	5	39
35	46°47′	300	12	68	147	.277	90	92	0	0	0	0	24	0	7
4	44°00′	400	20	70	139	.294	86	100	0	0	4	0	5	5	18
9	41°58′	1,050	25	71	131	.329	100	100	0	0	0	8	30	39	74
24	44°50′	120	18	68	130	.362	96	88	0	0	0	9	48	0	19
6	42°20′	2,300	23	67	130	.308	94	100	0	0	0	0	60	31	63
29	46°15′	1,000	9	70	128	.382	100	90	0	0	0	0	38	0	7
37	45°50′	300	14	67	126	.320	86	95	0	0	0	0	7	0	40
38	45°50′	600	8	67	122	.272	88	75	0	0	0	0	11	0	0
1	42°55′	500	21	69	117	.320	100	100	0	0	0	0	32	4	12
27	46°35′	800	16	66	114	.295	88	75	0	0	0	0	12	4	44
34	46°20′	1,500	7	65	111	.306	85	72	0	0	0	0	17	21	40
36	44°07′	1,550	16	65	111	.264	86	90	0	0	0	0	26	0	12
2	44°15′	1,950	15	66	109	.275	97	93	0	0	0	3	13	21	11
30	46°00′	1,600	9	66	109	.247	84	66	0	0	7	4	52	0	19
28	46°35′	800	14	65	107	.295	96	77	0	0	0	0	48	9	40
3	43°20′	1,950	17	64	106	.247	96	100	0	0	0	0	32	11	0
5	44°00′	2,100	15	63	98	.281	92	82	0	0	0	0	28	0	27

[1]After 62 days, all plants growing on nightlengths of 10 hours or less were still active.
[2]In this treatment, the weak-light period preceded the period of high intensity light; evidently this made it less effective than in cases where it followed the high-light period.
[3]Single tree collection.

nightlengths.

Both nightlength and seed source (environment and heredity) affected this timing of bud formation, which essentially stopped terminal elongation. For any given source, seedlings tend to form buds earlier under long nightlengths than under short nightlengths. But for any given nightlength, seedlings of northern parentage tend to stop growing earlier than those of southern parentage.

For example, after 77 days more than half the plants of low-elevation North Carolina sources (12 and 13, estimated frost-free seasons near 190 days) still had active stem tips under nightlengths as long as 11 hours. A low Tennessee source (17) showed a regular increase in the percentage of active plants, from 0 under 12-hour nightlength to 100 under 4 hours. On the other hand, for most sources from regions with growing seasons of less than 164 days, all plants had stopped growth under nightlengths of 9 hours or greater; many plants had gone dormant, even under 8- and 4-hour nightlengths.

Stem elongation. The differences in duration of growth were mainly responsible for the differences in total height above the cotyledons, although differences in the rate of elongation also affected height growth. Figure 2A shows the gradation of decreasing total height with increasing nightlength. Comparisons with other parts of Figure 2 show the striking differences related to source. Under either 4- or 12-hour nightlengths, plants of southern sources (2A, 2D) and sources from middle latitudes near the Atlantic coast or Lake Michigan (2C), all of which have relatively long frost-free seasons, grew considerably more than plants from generally northern sources having short growing seasons (2B).

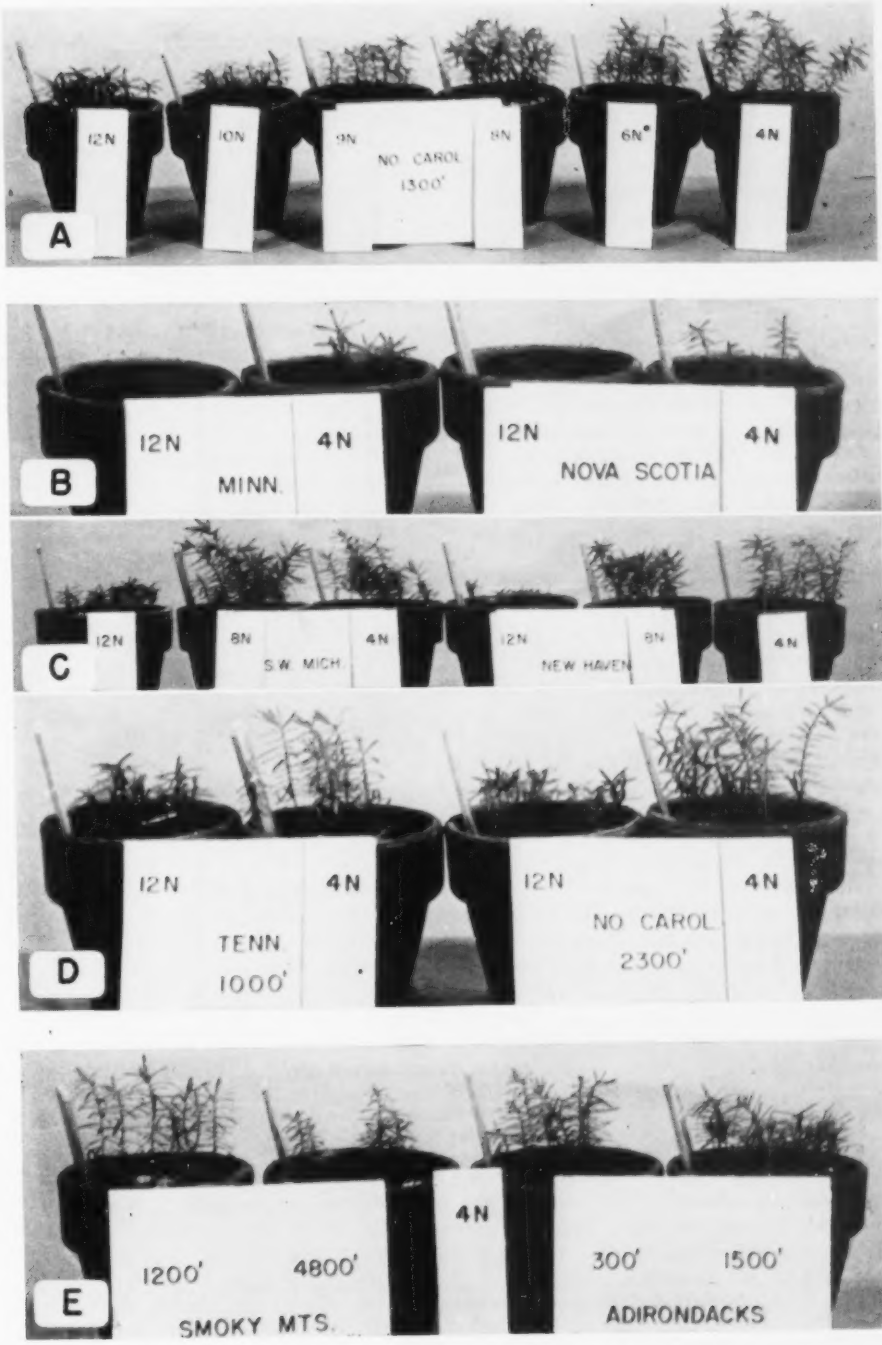
Similar differences are shown for seedlings of sources in the same latitude, but different altitude. Figure 2E shows seedlings under 4-hour nightlength, for the Great Smoky Mountains in the south and the Adirondack Mountains in the north. In each case the low-elevation (long-season) sources grew more than the high-elevation (short-season) sources.

Figure 1 shows the influences of both latitude and altitude of source region on the quantitative trend in seedling growth, averaging over all treatments. Average elongation exceeded 14 mm only for low-elevation North Carolina sources. It exceeded 10 mm for coastal Connecticut, New Jersey, southern New York, southern Michigan, Ohio, and Tennessee sources, with the exception of the high elevation source from the Great Smokies. Seedlings of this source, and most of the sources throughout the main belt of hemlock forests from Nova Scotia to Minnesota, had mean elongation between 6 and 10 mm, while a few Canadian sources and that from Franconia Notch, N.H., averaged less than 6 mm.

Since these seedlings were grown together in essentially identical environments, it would seem natural to conclude that any differences that were statistically significant were due to genetic diversity within the species. This conclusion would seem all the more convincing in view of the natural geographic pattern outlined in Figure 1.

The differences in elongation among sources might, however, be due merely to the increase in growth with seed weight, which is conspicuous in Figure 3A. The

FIGURE 2. *Influence of photoperiod and seed source on hemlock growth (pots all 3½ inches wide).* A. *Effects of varying nightlength (N hours of darkness out of 24) for seed source 13.* B–D. *Examples of hemlock growth on long and short night periods for a wide range of hemlock sources, east to west and north to south:* B. *Northern sources with short growing seasons (29 and 22).* C. *Mid-latitude sources (33 and 7) with long growing seasons.* D. *Southern low-elevation sources (15 and 13).* E. *Effects of altitude and latitude on growth of hemlocks under favorable (4-hour night) conditions. Sources 17 and 18 in Great Smoky Mountains; 4 and 36 in the Adirondacks.*


A
12N
10N
9N
NO. CAROL
1300'
8N
6N
4N
B
12N
4N
MINN.
12N
4N
NOVA SCOTIA
C
12N
8N
4N
S.W. MICH.
12N
8N
4N
NEW HAVEN
D
12N
4N
TENN
1000'
12N
4N
NO. CAROL
2300'
E
4N
1200'
4800'
SMOKY MTS.
300'
1500'
ADIRONDACKS

apparent relation to frost-free season might conceivably be an illusion brought about by the tendency for seeds to grow larger in regions of longer seasons, as shown in Figure 3B and Table 1. On the other hand, the relation of growth to frost-free season seems (Fig. 3C) to be even closer than its relation to seed weight, and this could not be explained completely by the correlation of seed weight and season.

To clarify this point, the following statistical approach was used. Table 2 shows that the separate regressions of the logarithm of mean growth to 100-seed weight, b_{zy}; of weight to frost-free season, b_{yx}; and growth to season, b_{zx}, are all statistically significant; in each case, variances accounted for by regressions, B^2, are significantly greater than variances due to the scatter around these respective lines, as might be expected from observing Figures 3A, 3B, and 3C respectively.

To estimate effects of season independent of seed weight, and of seed weight independent of season, we need the partial regressions, $b_{zx.y}$ and $b_{zy.x}$ (Table 3). In the case of the 8-hour night treatment illustrated in Figure 3C, we see that the first of these,

$$b_1 = b_{zx.y} = c_{11}[zx] + c_{12}[zy] = .004,271$$

is indeed very much larger than the second,

$$b_2 = b_{zy.x} = c_{22}[zy] + c_{12}[zx] = .000,773$$

where the c's are the elements of the inverse matrix given in Table 3. Compared with the corresponding simple regressions, regression on seed weight now appears considerably less important than it did before. The sum of squares accounted for by *both* partial regressions,

$$\Sigma B^2 = B^2_1 + B^2_2 = b_1[zx] + b_2[zy] = .700,358$$

is only slightly greater than that accounted for by the simple regression on frost-free season alone,

$$B^2_{zx} = b_{zx}[zx] = .678,949$$

The difference between these, .021,409, is not statistically significant compared with the chance variance $s^2 = .013,446$ due to scatter around the line, even in the case of the 8-hour night treatment where this term is relatively large.

Thus partial regression analysis did, indeed, reveal a distortion in the apparent importance of the two factors of season and seed weight, due to the fact that they are correlated with one another. But instead of unfairly exaggerating the effect of season because of a real effect of seed weight, it seems now that their correlation resulted in an exaggeration of the apparent influence of seed weight because of the real effect of season. This result thus eliminates the most obvious objection to the interpretation of the differences in seedling

TABLE 2. Simple regressions relating elongation, seed weight, and frost-free season of seed source region.[1] *(Sixteen-hour day—8-hour night photoperiod treatment used as example.)*

	Frost-free season	Wt. of 100 seed mg	Log mean epicotyl elongation	
Mean	$\bar{x} = 142.833$ days	$\bar{y} = 316.4$ mg.	$\bar{z} = 1.158,233$	
Variance	$[x^2] = 27708$	$[y^2] = 57185$	$[z^2] = 1.063,403$	
Cross-products		$[yx] = 24346$	$[zy] = .148,198$	$[zx] = 137.158$
Slopes		$b_{yx} = .878,663$	$b_{zy} = .001,551$	$b_{zx} = .004,950$
Variance due to regression		$B^2_{yx} = 21392$	$B^2_{zy} = .229,915$	$B^2_{zx} = .678,949$
Sums of squared deviations around regression		$[y^2] - B^2_{yx} = 35793$	$[z^2] - B^2_{zy} = .833,488$	$[z^2] - B^2_{zx} = .384,454$
Variance around regression		$s^2_y = 1278$	$s^2_z = .029,767$	$s^2_z = .013,730$
Variance ratio (all significant at 1% level, F .01 (1, 28) = 7.64)		16.738	7.72	49.45

[1]Brackets in table denote sums of deviations around means, e.g.,
$[x^2] = \Sigma(x-\bar{x})^2 = \Sigma x^2 - (\Sigma x)^2/N$, $[zx] = \Sigma(z-\bar{z})\ (x-\bar{x}) = \Sigma zx - (\Sigma z)\ (\Sigma x)/N$.

TABLE 3. Regressions and variances for separate photoperiodic treatments.

Statistical computations[1]		Nightlength[2] in hours					
		4	8	9	10	11	12
Mean elongation	$\bar{x}$	1.265	1.158	.889	.831	.836	.766
Simple regressions							
On season	b_{xs}	.004,523	.004,950	.004,301	.003,294	.002,777	.002,447
On 100 seed weight	b_{xy}	.001,297	.001,551	.001,225	.001,047	.000,934	.000,712
Partial regressions[3]							
On season	$b_1 = b_{xs.y}$	.004,184	.004,271	.003,998	.002,802	.002,247	.002,230
On 100 seed weight	$b_2 = b_{xy.s}$	.000,385	.000,773	.000,346	.000,560	.000,603	.000,240
Total scatter around mean	$[x^2]$	.789,940	1.063,403	.786.688	.538,917	.504,741	.371,130
Due to season and weight							
$\Sigma B^2 = b_1\ [sx] + b_2\ [sy]$		.572,087	.700,358	.516,921	.311,942	.226,788	.167,138
Added by seed wt.	$B^2 - b_{xs}[sx]$	.005,315	.021,409	.004,276	.011,220	.013,068	.001,656
Residual scatter	s^2	.008,069	.013,446	.009,991	.008,406	.010,295	.005,555

[1]Brackets indicate sums of products or squared deviations around the means.

[2]Nightlengths in these treatments varied only in duration of a supplementary dim light *following* a period of 12 hours of bright light common to all treatments.

[3]Computed from the following elements of the inverse matrix: $c_{11} = [y^2]/D = .000,057,660,452$, $c_{12} = [xy]/D = .000,024,548,419$, $c_{22} = [x^2]/D = .000,027,938,372$, where $D = -[xy]^2 + [x^2]\ [y^2] = 991754264$.

growth as being due primarily to some real genetic difference that is systematically related to the climate of the region where the parents had grown.

As would be expected from the differences in timing of bud formation (Table 1), there were differences in growth for seedlings of all sources, related to nightlength. This is clearly shown by the shift in position of the regression lines in Figure 3D. The main differences were in the general level of growth, but there seem to be differences in slope as well.

Partial regression computations were made also for the other photoperiodic treatments and are shown in the columns of Table 3. In these, variances accounted for by seed weight, over and beyond that accounted for by frost-free season alone, were even smaller than in the preceding example for an 8-hour night. As a result, the effect of seed weight is clearly not significant when tested in an analysis of variance (Table 4) for all six regression lines.

This overall analysis also provides a test of whether the regressions of growth on season for different photoperiodic treatments, graphed in Figure 3D, represent essentially parallel lines or differ significantly in their slopes. The very large variance accounted for by a single common slope, i.e., the "main effect" of season, certainly suggests a strong approach to parallelism. Nevertheless, the interaction of slope with treatment, based on the five degrees of freedom between treatments, is significant at the level of .025 and indicates a real heterogeneity among slopes. This is relevant to the later discussion of whether all sources can be considered as having the same "critical nightlength" for bud formation.

The preceding tests are based on the pooled estimate of scatter or chance variation based on the 27 degrees of freedom for each of 6 treatments, for a total of 162 degrees of freedom. Bartlett's tests for heterogeneity among variances indicated that they were not significantly different for these 6 treatments. This conclusion suggests incidentally that the transformation of the arithmetic mean elongations to logarithms was quite effective in eliminating the large difference in variance that would have arisen if the analysis had been made on the untransformed means on an arithmetic scale. (Later analyses have reached essentially similar conclusions using the means of the logarithms of the individual data, instead of the logarithms of the arithmetic means which were used here.)

The tendency for seedlings of northern origin to make less growth than do those of southern origin, which was clear for all the nightlength treatments at 17°, was also evident at various temperature treatments that were all maintained with an 8-hour nightlength. However, the quantitative differences in growth were generally not as great as at 17° for a variety of reasons.

At the very low temperature of 7°, the whole process of growth was so slow that plants remained active a long time while making relatively little height growth, even in the case of long-season sources. In this one case, there was a significant partial regression of growth on seed weight, beyond what could be acounted for by season alone. Probably the reasons for this

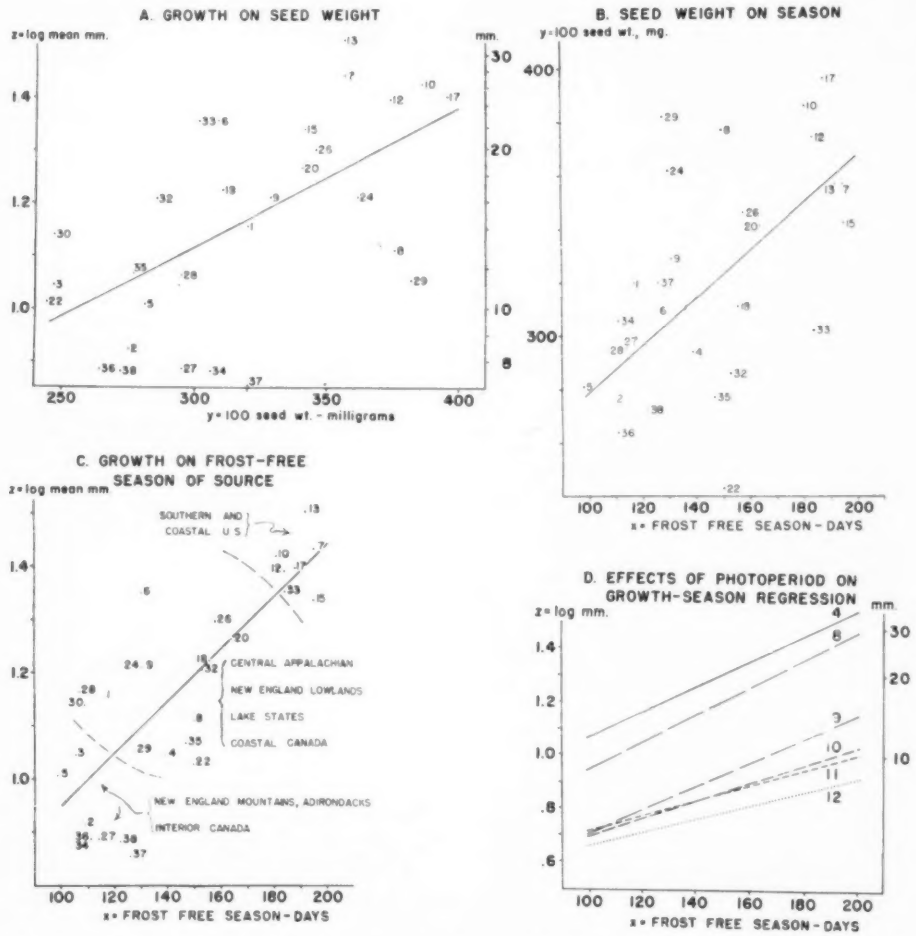

A. GROWTH ON SEED WEIGHT
z = log mean mm.
mm.
y = 100 seed wt. - milligrams
B. SEED WEIGHT ON SEASON
y = 100 seed wt., mg.
x = FROST FREE SEASON - DAYS
C. GROWTH ON FROST-FREE SEASON OF SOURCE
z = log mean mm
SOUTHERN AND COASTAL U.S.
CENTRAL APPALACHIAN
NEW ENGLAND LOWLANDS
LAKE STATES
COASTAL CANADA
NEW ENGLAND MOUNTAINS, ADIRONDACKS
INTERIOR CANADA
x = FROST FREE SEASON - DAYS
D. EFFECTS OF PHOTOPERIOD ON GROWTH-SEASON REGRESSION
z = log mm.
mm.
x = FROST FREE SEASON - DAYS

FIGURE 3. *Regressions relating z, the logarithm of mm of elongation above cotyledons; y, the weight of 100 seeds in mgs; and x, the frost-free season of the region of the parent source to one another.* A, B, *and* C *represent simple regressions of z on y, y on x, and z on x, for 30 sources at a single nightlength of 8 hours.* D *shows how the regression of z on x varies with nightlength, both in mean level and slope.*

TABLE 4. Analysis of variance of regression of growth, z, on seed weight, y, and estimated frost-free season of source region, x, under six experimentally controlled nightlengths.

Source of variation	Sum of squares	D.F.	Mean square
Duration of night	6.206,954	5	1.241,391**
Regression on frost-free season			
Slope common to all treatments	2.293,763	1	2.293,763**
Difference among slopes	.134,527	5	.026,905*
Added by regression on 100-seed weight	.056,950	6	.009,491
Residual scatter	1.505,584	162	.009,294

**Effects of nightlength (environment) and frost-free season of region of parent stand (heredity) both highly significant.

*Interaction of regression on season for varying nightlengths (possible indication of different critical nightlength among sources) is significant at .025 level of probability.

Regressions of growth on seed weight, over and above the variance accounted for by frost-free season alone, are not significant.

TABLE 5. Epicotyl elongation at different combinations of day and night temperatures.

Day temp. (°C)	Night temperature (°C)						
	7	12	17	22	27	32	37
			A. Regression on frost-free season				
37			2.261		1.949		[1]
32				2.226		2.948	
27		3.307	4.128		2.669		
22		3.373		2.612			
17	2.672		4.950		2.413		
12	3.528						
7	.588						
			B. Mean log elongation				
37			1.110		1.0982		[1]
32				1.115		.960	
27		1.119	1.207		1.140		
22		.965[2]		.973[2]			
17	.761		1.137		1.207		
12	.615						
7	.470						

[1]All plants died.
[2]Poor elongation of some 22° plants can probably be discounted as due to accidental drying.

were the rather slight progress beyond the cotyledon stage, the unfavorable temperature for photosynthesis of new food, and the consequently greater reliance on stored food, which would be supplied mainly by the seed.

Also, at relatively high temperatures, especially at high night temperatures, the formation of buds was later than at 17° constant temperature. While seedlings from

short-season source regions tended to go dormant earlier than the others, the difference was less striking than at 17°; evidently cool temperature as well as long nightlength enhances bud formation, and plants from short-season sources are more sensitive to this influence. On the other hand, very high temperatures like 32° or 37° tend to suppress the *amount* of elongation, even though plants continue to grow a longer time than at 17°. While seedlings of long-season origin grew taller than the others, this stunting tended to diminish their superiority in height growth. Thus differences among sources in both the duration and amount of elongation are smaller under these conditions.

The spread in elongation between long- and short-season sources for varying combinations of day and night temperature is summarized numerically by the regression coefficients (slopes) in Table 5A. These are greatest at 17° constant and 27° day-17° night temperatures, and decrease for both low and high temperatures, as just stated.

The mean elongation, averaging over all sources, is given in Table 5B. This shows that daily temperature alternations between 17° and 27° are somewhat more favorable for elongation than either 17° or 27° constant temperatures, as is typical for plants showing a thermoperiodic response. Higher and lower temperature both tended to decrease total elongation.

Discussion

Eastern hemlock seedlings illustrate especially well the influence of the different factors which regulate the growth and dormancy of trees. First, stem elongation eventually ceases, even under the most favorable environmental conditions, probably because of some inherent physiological mechanism that becomes effective as the season progresses. Secondly, nightlengths exceeding 8 or 9 hours tend to accelerate bud formation and hardening off of stems both in our experiments and in the field. Nursery seedlings of most sources commonly develop terminal buds around mid-August (in southern Connecticut), at the time when natural nightlength is just increasing beyond 9 hours, including an hour of twilight. Thirdly, cool temperature also apparently helps to hasten bud development. In addition, it is well known that many unfavorable environmental conditions such as drought or nutrient deficiency can further hasten the termination of growth.

The differences in the duration of growth of the plants from different seed origins undoubtedly are the results of adaptation to a combination of these environmental factors rather than one alone. Furthermore, an additional controlling factor is indicated by the fact that the regression of elongation on frost-free season is similar under all the experimental environments used. This factor presumably acts through the inherent physiological mechanism mentioned, and is independent of the control by photoperiod or other external factors. It must be similar to the "endogenous mechanism" emphasized by Wareing (1956).

On the other hand, this does not exclude the possible importance of differences among provenances in the so-called "critical nightlength." The term implies a nightlength at which a small increment in length has a *relatively* greater effect on bud formation than changes at either longer or shorter nightlengths, without necessarily implying a very abrupt threshold. In Table 1, we noted that some seedlings of long-season origin tended to remain active on nightlengths exceeding 9 hours even after almost all of the short-season seedlings had gone dormant under this light regime. The differences in slope of regression lines (Fig. 3D, Tables 3, 4) also suggest that there is relatively more spread in growth between 9-, 10-, 11-, and 12-hour nightlengths among long-season seedlings and less between 4- and 8-hour nightlengths than there is for short-season seedlings. Further statistical analysis elsewhere (Olson *et al.* 1959) bears out the implication of a slight but real difference among sources in "critical nightlength." Nightlengths only slightly longer than 8 hours seem to have greatest effect in hastening

bud formation on seedlings of northern origin, while nigthtlengths approaching 9 hours may be most effective for seedlings of southern origin.

Such a small difference might seem inconsequential if it were not true that nightlength changes rather rapidly in late summer. Under a given changing photoperiodic regime, a difference of a quarter or half an hour in the "critical" nightlength might make the short-season genotypes go dormant 5 or 10 days earlier than the long-season genotypes. Thus differences in response to photoperiod may be reinforcing whatever natural tendency exists for these genotypes to differ in the timing of bud formation and hardening off *irrespective of photoperiodic control.* But we cannot be sure of the relative importance of these two modes of control.

In natural conditions, the additional effect of cool temperature would also hasten bud formation in northern plantations as compared with southern ones. Furthermore, the greater "spread" among sources in time and amount of growth at 17° C as compared with higher temperatures, which is represented by the higher regression coefficients in Table 5A, suggests that northern genotypes are more likely to go dormant at these moderately cool temperatures than southern ones even when photoperiods are favorable. This additional factor further reinforces the genetic differences related to inherent physiological control and to photoperiodic regime.

In view of the ever-present competition under field conditions, we can readily understand why seedlings which tend to make the most growth would survive natural selection and pass this trait on to future generations. Presumably hemlock, as well as other species (e.g. Bates 1930, Langlet 1938, Sylven 1940), has by this selection become adapted to the most complete utilization of the long frost-free season of southern and coastal regions.

Of course, any benefit from excess growth would be cancelled if plants remained active until the tender stem tissue was exposed to early autumn frost. Such damage has indeed been evident for several years in southern seedlings grown near New Haven, Conn., and dieback is beginning to counteract their initial advantage in height growth in many cases. Seedlings grown in Wisconsin from this nursery showed even more striking differences in frost injury. The amount of damage had a highly significant positive correlation with the growing season at the point of origin and with the amount of elongation under the 9-hour night treatment of the present experiment (Nienstaedt 1958). In the north, early bud formation and hardening off has presumably been more advantageous than the extra height growth of southern seedlings. Thus any local population is subject to natural selection by opposing tendencies, and it is the balance of these which conditions the normal duration of the growth period.

The gradation in the timing and amount of growth shown in Figures 1 and 3 suggests that the pattern of genetic change is a cline and follows the gradual shift in climate over the species range. In some places, as for example in the Great Smoky Mountains, large climatic differences occur over short distances. The hemlock population in some of these areas is almost continuous so that a free exchange of genes is possible along the intervening mountain slopes. Nevertheless, genetic differences may have been maintained by continuous natural selection which counteracts the dilution of genes in the population at one end of the climatic gradient by those from the other, even where short distances are involved.

The sampling of the diversity within the species in this study hardly is intensive enough to prove definitely the existence of a single cline or to exclude the possibility of abrupt genetic discontinuities along some portions of the geographic gradient within the distribution. Hemlock in particular often occurs in groves which are isolated by physiography or disturbance history. Genetic discontinuities are apt to arise in such isolated populations. Squillace and Bingham (1958) have recently shown very localized genetic isolation of western white

pine in areas of abrupt contrasts in topographic relief and in site quality. Quite possibly, intensive studies would find similar differences in hemlock, especially in those parts of its range in New England and certain higher portions of the Appalachian Mountains where it may occupy poor ridge sites as well as favorable coves.

As long as a strong possibility remains that both gradual and relatively abrupt genetic changes occur within a species population, it seems premature to draw a rigid contrast between clinal and "ecotypic" variation, ecotype implying discontinuity. Until much more is known about genetic patterns of a large number of characteristics of hemlock and of most other species that have been studied intensively, it may be advisable to use the term "ecotype" without a strict connotation of isolation.

The correlation between seed weight and early growth of seedlings has received considerable attention in the literature and has been summarized by Hough (1952b). Often seedlings from large seed tend to be larger and heavier than those developing from light seed. However, the correlation between seed weight and the growing season at the point of seed origin is also a common one (Langlet 1938, Bates 1930, Baldwin 1942). Perhaps some of the differences that have been attributed to seed weight belong in small or large part to other genetic factors, which evolved through an adaptation to the length of the frost-free period.

Such confounding of variables can in part be overcome by the partial regression analysis used here. For example, this technique applied to Hough's red pine data showed a significant effect due to growing season ($F = 22.00$). In his data, however, unlike the hemlock data, there was also a significant regression due to seed weight ($F = 5.1$).

Aside from the statistical, physiological, and genetic interpretations of these differences, one can readily see the practical implications for those who are interested in planting hemlock for ornamental or forestry purposes. Probably most commercial hemlock seed comes from relatively northern sources, in the main belt of hemlock-northern hardwood forests. In states with generally milder climate, as in Connecticut where more than half a million hemlocks are currently being grown in nurseries, stock from these sources is likely to grow more slowly in nurseries, and perhaps later in life, than seedlings of local origin. Southern Appalachian seed, occasionally marketed in the north, is likely to produce plants that are more subject to frost injury and foliage discoloration than local stock.

In mountainous regions and near large bodies of water where considerable climatic differentials occur within relatively small areas, transfer of stock over small distances may result in considerable loss of production and damage from frost. This of course has been demonstrated for other tree species; the magnitude of such losses remains to be determined by field studies in each case.

Summary

Eastern hemlock seedlings from 30 sources were grown under controlled daylength and temperature conditions. They showed that:

1. On any given regime of day- and nightlength, seedlings from a source region with a long frost-free season tend to form buds and stop elongation later than those from a region of short frost-free season. The 30 sources showed a distinct clinal variation in photoperiodic responses, but this does not exclude the possibility of relatively abrupt genetic changes either on a broad or local geographic scale.

2. Seed weight was also dependent on the length of growing season at the point of origin. This correlation tended to exaggerate the apparent regression of height on seed weight. A partial regression analysis, however, shows that the effect of seed weight was generally negligible.

3. Hemlock has a continuous gradation in response to varying nightlengths, shorter nightlengths permitting longer growth. The "critical" nightlengths showing the greatest influence on growth seems to lie

in the range of 8 to 9 hours, probably nearer 8 hours for seedlings of regions of short frost-free seasons and nearer 9 hours for seedlings of long-season sources.

4. Height growth also is influenced by temperature in several ways. Constant high or low temperatures retard growth. The unfavorable effects of high day temperatures are counteracted by lower night temperatures, with 27° C day and 17° C night nearly ideal.

5. Although field progeny tests of forest tree ecotypes are necessary to assess the ultimate value of the various genotypes of trees, short-term studies with seedlings under controlled conditions may give valuable early indications of responses to environment and the amount and type of genetic variation within a species; they can separate effects of heredity and environment and show their interactions in a way that is not possible in the field.

Literature Cited

BALDWIN, H. I. 1942. Forest tree seed. 240 pp., illus. Chronica Botanica Co., Waltham, Mass.

BATES, C. G. 1930. Why nurserymen prefer southern seed. J. For. 28: 232-233.

CRITCHFIELD, WILLIAM B. 1957. Geographic variation in *Pinus contorta*. Maria Moors Cabot Foundation Pub. 3, 118 pp., illus.

DOWNS, R. J., and H. A. BORTHWICK. 1956. Effects of photoperiod on growth of trees. Bot. Gaz. 117: 310-325, illus.

GEVORKIANTZ, S. R., and E. I. ROE. 1935. Photoperiodism in forestry. J. For. 33: 599-602.

HOUGH, A. F. 1952a. Preliminary results of red pine seed-source tests in northwestern Pennsylvania. U. S. For. Serv. Northeast. For. Expt. Sta., Sta. Paper 49, 28 pp., illus.

———. 1952b. Relationships of red pine seed source, seed weight, seedling weight, and height growth in Kane test plantation. U. S. For. Serv. Northeast. For. Expt. Sta., Sta. Paper 50, 14 pp., illus.

IRGENS-MOLLER, HELGE. 1957. Ecotypic response to temperature and photoperiod in Douglas-fir. For. Sci. 3: 79-83, illus.

KRAMER, PAUL J. 1936. Effect of variation in length of day on growth and dormancy of trees. Plant Physiol. 11: 127-137, illus.

———. 1937. Photoperiodic stimulation of growth by artificial light as a cause of winter killing. Plant Physiol. 12: 881-883, illus.

———. 1957. Some effects of various combinations of day and night temperatures and photoperiod on the length growth of loblolly pine seedlings. For. Sci. 3: 45-55, illus.

KRIEBEL, HOWARD B. 1957. Patterns of genetic variation in sugar maple. Ohio Agric. Expt. Sta. Res. Bull. 791, 56 pp., illus.

LANGLET, O. 1938. Proveniensförsök med olika trädslag. Svenska Skogs Fören. Tidskr. 36: 55-278, illus.

———. 1942-1943. Photoperiodismus und Provenienz bei der gemeinen Kiefer (*Pinus silvestris* L.), Medd. Från Statens Skogsförsöksanstalt 33: 294-330, illus.

MUNGER, THORNTON T. 1947. Growth of ten regional races of ponderosa pine in six plantations. U. S. For. Serv. Pacif. Northwest For. Expt. Sta. For. Res. Note 39, 4 pp.

——— and G. MORRIS. 1936. Growth of Douglas-fir trees of known seed sources. U. S. Dep. Agric. Tech. Bull. 537, 40 pp., illus.

NIENSTAEDT, HANS. 1958. Height growth is indicative of the relative frost resistance of hemlock seed sources. U. S. For. Serv. Lake States For. Expt. Sta. Tech. Note 525, 2 pp., illus.

OLSON, J. S., and HANS NIENSTAEDT. 1953. Hemlock in Connecticut. Frontiers of Plant Sci. 6: 8.

——— and HANS NIENSTAEDT. 1957. Photoperiod and chilling control growth in hemlock. Science 125: 492-494, illus.

———, FOREST W. STEARNS, and HANS NIENSTAEDT. 1959. Eastern

hemlock seeds and seedlings—response to photoperiod and temperature. Conn. Agric. Expt. Sta. Bull. 620, 70 pp., illus.

PAULEY, SCOTT S., and THOMAS O. PERRY. 1954. Ecotypic variation of the photoperiodic response in Populus. J. Arnold Arbor. 35: 167-188, illus.

RUDOLF, PAUL O. 1947. Importance of red pine seed source. Soc. Amer. For. Proc. 1947: 384-398, illus.

————. 1953. Forest genetics work at the Lake States Forest Experiment Station. *In* Lake States For. Genet. Conf. Proc. 1953. U. S. For. Serv., Lake States For. Expt. Sta. Misc. Rept. 22: 1-10.

SCHANTZ-HANSEN, T., and R. A. JENSEN. 1952. The effect of source of seed on growth of jack pine. J. For. 50: 539-544, illus.

SCHMIDT, WERNER. 1951. Kurzfristige Herkunftsteste bei der Kiefer. Forstarchiv 22: 50-52.

SQUILLACE, A. E., and R. T. BINGHAM. 1958. Localized ecotypic variation in western white pine. For. Sci. 4: 20-34, illus.

SYLVEN, N. 1940. Lång-och Kortdagsväxter av de svenska skogsträden. Meddel. Från Föreningen För Växförädling av Skogstrad. Svensk Papp. Tidn. 43: 317-324, 332-342, 350-351, illus.

SYRACH LARSEN, C. 1949. Forest genetics. Third World For. Congr. Proc. No. 1, 9 pp. (Original pagination not shown in reprint.)

WAKELEY, PHILIP C. 1944. Geographic source of loblolly pine seed. J. For. 42: 23-32.

————. 1954. Planting the southern pines. U. S. Dept. Agric. Monog. 18, 233 pp., illus.

WAREING, P. F. 1948. Photoperiodism in woody species. Forestry 22: 211-221.

————. 1950. Growth studies in woody species. I. Photoperiodism in first-year seedlings of *Pinus silvestris*. Physiol. Plant. 3: 258-276, illus.

————. 1956. Photoperiodism in woody plants. Ann. Rev. Plant Physiol. 7: 191-214.

WEIDMAN, R. H. 1939. Evidences of racial influence in a 25-year test of ponderosa pine. J. Agric. Res. 59: 855-887, illus.

Erratum

In the article "Asymmetric Distribution of a Substance Found in Horizontally Displaced Eastern White Pine Leaders which Reacts with Salkowski Reagent," FOREST SCIENCE, Volume 6, Number 3, HCL concentration in Footnote 2 on page 243 should read 6.1 M (not 11.6).

Suggestions to Contributors

An article submitted for publication should be the best the writer is capable of producing, with all statements, tables, quotations, names and formulas verified before submission. The careful author will have his typescript reviewed by colleagues.

Articles should be typewritten, with 1½-inch margins, on one side only of white bond paper, size 8½ by 11 inches, or 8 by 10½ inches. Carbon copies are not acceptable. All copy should be double-spaced. Pages should be numbered consecutively, preferably in the upper right-hand corner. Only words intended to be set in italics should be underlined.

Material such as equations that exceed 42 spaces on the typewriter cannot be carried in a single line. Such material should either be set so that it can be broken into two or more lines, or should be presented in tabular form.

Tables

Each table should be typewritten on a separate sheet, given a title at the top, and should be numbered consecutively. Even if only one table is submitted, it should be designated Table 1.

Footnotes used in tables should be designated by numerals, never by asterisks or other typographical symbols. These footnotes should be typewritten as part of the table.

Illustrations and Figures

An illustration — whether a photograph, a line drawing, a map, or a graph — is designated as a figure. A caption should be submitted for each illustration, but the caption should be typewritten on a separate sheet.

All figures should be numbered consecutively. If only one is submitted it should be designated Figure 1. On the margin or back of each illustration should be written lightly in soft pencil the number of the figure, the name of the author, and an abbreviated title.

Photographs should be sharp and clear, printed on glossy paper. They should not be smaller than 4 by 5 inches. Sizes 5 by 7 inches and 8 by 10 inches are preferable. Photographs should never be rolled or bent. Care should be taken in fastening photographs with paper clips which often make indentations that show up in reproduction.

Drawings, maps, charts, and graphs are reproduced as line engravings. They should be at least twice as large as they are to appear when reproduced, and should be drawn in india ink on heavy white paper, or tracing cloth.

Footnotes

To indicate a footnote, place a superior figure after the word that refers to the note. Consecutive numerals should be used, never asterisks. Separate the footnote from the text by running a line about one inch inward from the left margin of the type.

Use footnotes to give credit to unpublished material and communications. If only a few references to literature are made (less than one per 1000 words), complete literature citations may be given in footnotes rather than in a separate listing.

Literature Cited

In FOREST SCIENCE practice, references to literature citations are designated by the author's name and year of publication inserted in parentheses at the appropriate place in the text. If there are more than two authors, list only the senior author's name in the text with the abbreviation *et al.* Example: (Smith *et al.* 1954). Only published references should be given in *Literature Cited*. Periodical abbreviations should follow *Guide to the use of Forestry Abstracts*, Commonwealth Forestry Bureau, Oxford, England, 1950.

Nomenclature and Terminology

When a species is first mentioned in a paper its common name may be immediately followed by its italicized scientific name in parentheses, but this latter name need not be repeated.

As the authority for the exact spelling of tree names, FOREST SCIENCE follows *Check List of Native and Naturalized Trees of the United States (including Alaska)*, Agriculture Handbook 41, Forest Service, U. S. Dept. Agric., Washington, D. C., 1953.

For the spelling of other plant names, contributors should follow *Standardized Plant Names*, 2d Edition, J. Horace McFarland Company, Harrisburg, Pa. 1942.

Technical usage in forestry and allied fields follows *Forestry Terminology*, 3rd Edition, Society of American Foresters, Washington 6, D. C. 1958.

There are many style manuals available for the guidance of writers. One of the best is the *Style Manual* of the U. S. Government Printing Office, Washington 25, D. C. 1959.

Webster's *New International Dictionary* is the accepted authority for general spelling.